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The Effects of Petroleum Hydrocarbons on Chemoreception and Behavior in the Dungeness Crab 'Cancer Magister'

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The behavior of Dungeness crabs, Cancer magister, was observed to determine not only whether oil exposure produced behavioral effects, but also whether crabs could change their behavior to mitigate any exposure effects. Dungeness crabs clearly detected the presence of petroleum hydrocarbons but did not avoid oil under all circumstances.

The effects of oil exposure on chemoreception and feeding behavior in Dungeness crabs were determined after measuring the high sensitivity of the crabs to chemical food cues. After 24 h of continuous exposure to 0.3 mg/L of oil-contaminated water, the proportion of crabs showing changes in antennular behavior was significantly reduced. Within 1 hour after return to clean water the antennular response recovered. Field and laboratory experiments then examined how oiled sediment influenced predation on littleneck clams by Dungeness crabs. In field enclosures, crabs consumed more clams from oiled than clean sand. The potential difficulty in finding food due to chemosensory disruption by petroleum hydrocarbons was apparently offset by an oil-induced change in prey behavior. To the extent that oiled sediment renders prey species more vulnerable to crab predation and crabs switch prey, harvesting of vulnerable prey by crabs would reduce their representation in the benthic fauna and produce ecological effects far different than those predicted from a series of conventional toxicity tests.

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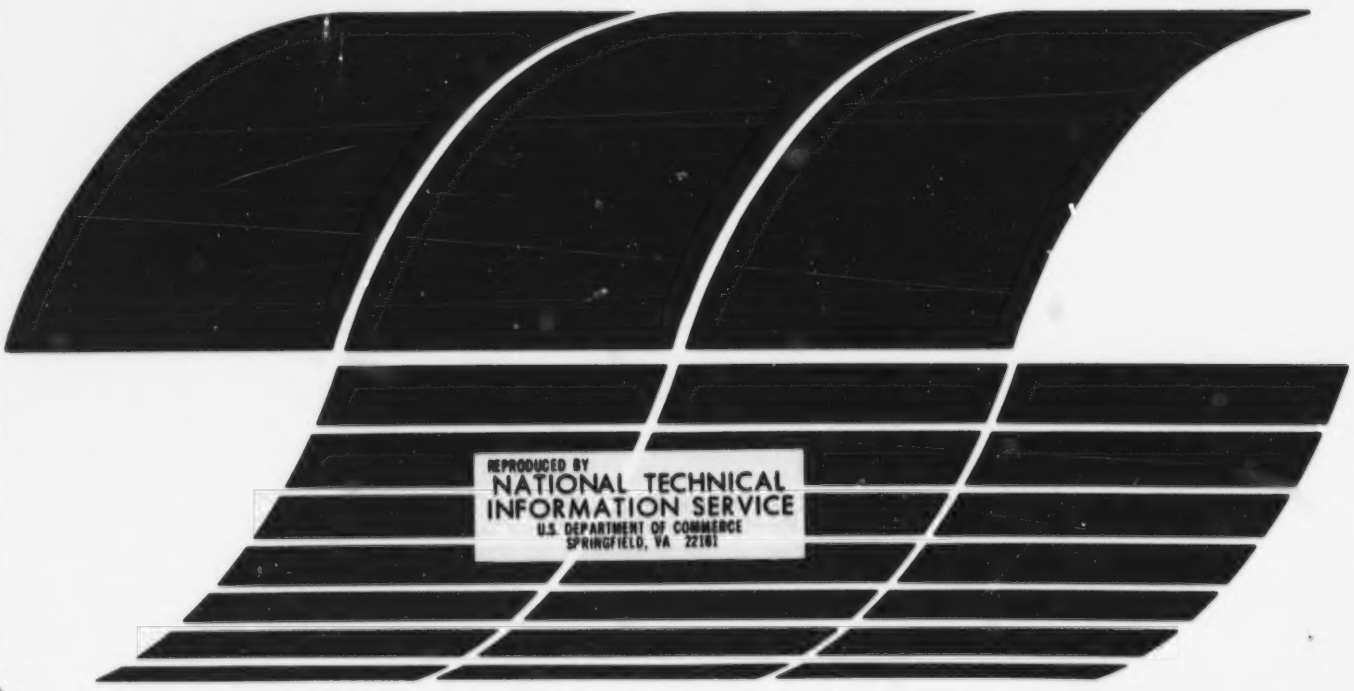

section, I.A., presents work soon to be published by Pearson, Sugarman, Woodruff, Blaylock, and Olla (1980b) and describes how Dungeness crabs detect dissolved petroleum hydrocarbons at concentrations below those typical of oil spills.

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THE EFFECTS OF PETROLEUM HYDROCARBONS ON CHEMORECEPTION AND BEHAVIOR IN THE DUNGENESS CRAB *CANCER MAGISTER*

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FOREWORD

The accelerated development of petroleum resources on the continental shelves of the United States, along with continued importation of petroleum from foreign sources, is expected to increase the transfer and refinement of petroleum in coastal areas. In order to properly evaluate the potential consequences of this increased petroleum flow, NOAA is conducting studies in the Fate and Effects of Petroleum Hydrocarbons in Selected Marine Organisms and Ecosystems. The overall objectives of this project are to study experimentally those specific processes controlling the distribution, transport, and effects (physiological, behavioral, and ecological) of petroleum hydrocarbons in coastal marine systems. These studies are expected to facilitate the assessment of environmental impacts of petroleum releases and to serve as the basis for developing regulatory measures for suitable protection of the marine environment. The study reported here addresses the question of whether chronic low-level petroleum inputs might interfere with critical, life-sustaining behavioral processes in a nearshore, commercially-important marine species. This report presents the results of three years of cooperative effort between B. L. Olla, Chief of Behavioral Investigations at NOAA, NMFS Sandy Hook Laboratory, Highlands, New Jersey, and W. H. Pearson of Battelle's Marine Research Laboratory, Sequim, Washington. Each section of the report represents work published, in press, or near final preparation for journal submission.

Douglas A. Wolfe
NOAA/Office of Marine Pollution Assessment

ABSTRACT

The behavior of Dungeness crabs, Cancer magister, was observed to determine not only whether oil exposure produced behavioral effects, but also whether crabs could change their behavior to mitigate any exposure effects. Dungeness crabs clearly detected the presence of petroleum hydrocarbons but did not avoid oil under all circumstances. Changes in the antennular behavior of crabs showed that they detected naphthalene at 10^{-2} mg/L and the water-soluble fraction of Prudhoe Bay crude oil at 4×10^{-4} mg/L. Thus, the crabs detected dissolved petroleum hydrocarbons at concentrations below those typical of oil spills. Behavioral observations of crabs given a choice between clean and oiled sand indicated that crabs avoided highly oiled sand (1000 - 2000 ppm) to some extent but spent more time in moderately oiled (<200 ppm) than clean sand. Because the extent of avoidance varied highly and was apparently related to factors intrinsic to the animal and its environment, we must assume that avoidance of oiled sand is not assured.

The effects of oil exposure on chemoreception and feeding behavior in Dungeness crabs were determined after measuring the high sensitivity of the crabs to chemical food cues. Abrupt changes in antennular orientation and sharp increases in antennular flicking rate indicated that crabs detected an extract of littleneck clam, Protothaca staminea, at 10^{-7} mg/L. At 10 mg/L of the extract crabs probed the substrate with the chelae or showed other feeding behavior. After 24 h of continuous exposure to 0.3 mg/L of oil-contaminated water and with oil still present, the proportion of crabs showing the changes in antennular behavior indicating detection of chemical food cues was significantly reduced. In contrast, the proportion showing chelae probing was not. Within one hour after return to clean water the antennular response recovered. Such rapid recovery suggests that the impairment was due to light anesthesia of chemosensory cells or, more likely, masking of food cue odor by oil. Petroleum hydrocarbons impaired the distance chemoreception seated in the antennules of Dungeness crabs and, thereby, could cause crabs some difficulty in finding food. Field and laboratory experiments then examined how oiled sediment influenced predation on littleneck clams by Dungeness crabs. In field enclosures, crabs consumed more clams from oiled than clean sand. A laboratory experiment indicated that the observed increase in predation derived in large part from increased prey accessibility due to an oil-induced change in clam burrowing behavior. The potential difficulty in finding food due to chemosensory disruption by petroleum hydrocarbons was apparently offset by an oil-induced change in prey behavior. To the extent that oiled sediment renders prey species more vulnerable to crab predation and crabs switch prey, harvesting of vulnerable prey by crabs would reduce their representation in the benthic fauna and produce ecological effects far different than those predicted from a series of conventional toxicity tests.

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INTRODUCTION

Changes in behavior have been shown to be quite sensitive indicators of environmental stress in marine animals (Olla, 1974; Olla et al., 1980a & b). Generally, behavioral studies of pollutant effects have simply substituted behavioral disruption for the normal end-point of death used in conventional toxicity assays. Rarely have these kinds of studies either choosen ecologically pertinent behavior for investigation or interpreted any observed behavioral changes on the basis of a thorough understanding of the organism's behavioral ecology (Olla et al., 1980a & b). Still, more rarely have such studies empirically followed the observed behavioral effects to their ecological consequence (see Ward & Busch (1976), Ward et al. (1976), and Krebs & Burns (1977) for examples of these rarer studies). In the work presented here we have addressed broader questions than just whether oil disrupts behavior and done so within a developing theoretical framework (Olla et al., 1980a & b) that points out the ecologically meaningful questions concerning behavioral ecological processes and the consequences of their disruption. Our aim in this work was to examine the effects of petroleum hydrocarbons on the behavioral ecology of adult Dungeness crabs, Cancer magister.

Our research took two pathways. One pathway examined whether Dungeness crabs could, within the scope of their genetically based norm of reaction, change their behavior to mitigate any effects of petroleum and, thereby, enhance the probability of survival. The other pathway investigated whether exposure to petroleum would produce untoward changes in some important behavior where the crab was unable to mitigate exposure behaviorally. The crab's failure to mitigate petroleum effects could derive from an inherent inability to change its behavior in the presence of petroleum or from an externally imposed inability to change behavior adaptively under particular environmental conditions. Research concerning behavioral mitigation of petroleum effects centered on laboratory experiments that measured the crab's ability to detect petroleum and then behave appropriately, i.e., avoid contact with oil-contaminated sand. Research concerning adverse petroleum effects centered on laboratory experiments that determined how petroleum modified chemosensory detection of food cues and field experiments that examined crab predation on a natural prey buried in oiled sand. The two sections of the report reflect our two pathways of research.

CONCLUSIONS AND RECOMMENDATIONS

Our results demonstrate that the Dungeness crab, Cancer magister, can detect dissolved petroleum hydrocarbons at concentrations well below those typical of oil spill situations. In so doing, the crab can meet the first prerequisite for any subsequent behavioral response that would mitigate any effects of oil exposure.

Whereas detection of petroleum hydrocarbons clearly occurred, whether the crab could behave appropriately after detection was not as clear. Avoidance of oiled sediment did occur but not under all circumstances. The extent of avoidance was not dramatic and seemed to vary as factors intrinsic to the crab, the oil, and the environment interacted. Petroleum hydrocarbons are one complex chemical stimulus among a host of other stimuli, both chemical and of other modalities. How the animal responds depends on where this complex stimulus is in a ranking that constantly changes as the animal's environmental needs change. The variation in activity level and pattern seen among the various experiments were related to variations in the phase relationships between tidal cycles and photoperiod and were one example of how the characteristics of the crab and the environment interacted.

Changes in the extent of avoidance with the oil concentration of the sand were noted. Crabs showed no difference between control and oiled sand in low concentrations (~20 ppm), seemed attracted to moderately oiled sand (~200 ppm), and avoided the highly oiled sand (~2000 ppm). These results suggest to us that the crab is capable of avoiding oiled sediment at high levels but that the occurrence and extent of avoidance depends on the environmental conditions and such factors as hunger level, reproductive condition, and migratory state, that are intrinsic to the crab. We must conclude, therefore, that it is presently best to be conservative and assume that avoidance of oiled sand is not assured.

In our laboratory studies of avoidance behavior in the Dungeness crab (Pearson et al., in prep.) and elsewhere with hake (Pearson et al., in prep.), and the blue crab (Pearson et al., in prep.), it is becoming increasingly clear that factors intrinsic to the animal and the environment apparently can override or at least lessen the extent of avoidance. Knowledge of these factors is crucial both to realistic experimental design and to meaningful extrapolation of laboratory results to the natural environment. Even our brief field observations coupled with the laboratory studies make us confident that more extensive study of crab behavior under natural conditions would enable us to develop a model that would indicate the circumstances under which crabs do and do not avoid oiled sand.

After establishing the acute sensitivity of Dungeness crabs to chemical food cues, we exposed crabs under continuous-flow for 24 h to petroleum hydrocarbons at concentrations typical of oil spill situations. Under the 24-h exposure, crabs showed impaired ability to detect chemical food cues. Recovery from impairment was observed one hour after ending exposure to oil-contaminated water. This rapid recovery suggested that either the hydrocarbons anesthetized the chemosensory cells or, more likely, masked

the food odor. Whichever the mechanism, the impairment would probably continue as long as petroleum hydrocarbons were present, and the continuing presence of petroleum hydrocarbons would likely make food finding difficult for the Dungeness crab. Because the crab detects dissolved petroleum hydrocarbons at 10^{-4} mg/L, we suspect that masking by even lower hydrocarbon levels than we tested could disrupt the sensing of chemical food cues, especially if the cues are quite dilute. Because even our brief exposure at one level produced a clear impairment in a chemosensory ability that supports a crucial process in the behavior and ecology of the crab, we feel that the effects of chronic low level exposure on chemosensory processes need study.

Whereas the observed impairment of distance chemoreception suggests that crabs would have more difficulty sensing prey, the field and laboratory experiments on crab predation unexpectedly showed crabs consuming more clams from oiled than clean sand. The potential difficulty in detecting prey by chemoreception in an oiled environment was apparently offset by a change in the burrowing behavior of the clam that increased prey accessibility. The implication of this change in prey accessibility is that whereas oiling of the sediment may not directly lead to the death of buried clams, oiled conditions could very well lead to serious inroads on the clam population by crab predation. It is still possible that under other oiled conditions, oiled sediment may act as a chemosensory barrier to the detection of buried prey. Our attempt to trace empirically an observed behavioral effect to its ecological consequences gave unexpected results that revealed the complexity of the situation. Our experience here only reinforces our view that the fruitfulness of examining pollutant effects rests on a comprehensive understanding of the behavioral ecology of all the organisms involved.

In the continual search for sublethal effects of petroleum hydrocarbons, there are clearly some sublethal effects on the Dungeness crab. Our studies have only revealed a small portion of these effects. Even so, we can clearly see how these observed effects influence the animal's relationship to its environment. Any attempt to predictively model the fate of Dungeness crabs under oil exposure must consider these demonstrated sublethal effects.

I. BEHAVIORAL MITIGATION OF PETROLEUM EFFECTS

A change in behavior is the initial response of an animal to an environmental perturbation (Slobodkin, 1968). If the behavioral response removes or lessens the effect of the perturbation, the probability of death or the cost incurred by other adaptive responses to maintain homeostasis may be lowered or eliminated. The response may be movement away from the area of the perturbation or other changes in behavior that effectively reduce exposure. Generally, it is a fair statement that behavioral mitigation of potentially stressful environmental changes is evident at almost all phylogenetic levels (for examples related to petroleum effects see Johnson, 1977; Olla et al., 1980a).

For a successful behavioral response to an environmental perturbation to occur, the animal must be capable of: 1) sensing it; 2) recognizing it as aversive; and 3) responding appropriately (Pearson & Olla, 1979; Olla et al., 1980a & b). In Figure 1, we have diagrammed possible response pathways that may occur when an animal is subjected to an environmental perturbation.

Obviously no behavioral act can be elicited if the perturbation is not sensed or is sensed at a level that will not permit the animal to respond behaviorally before becoming debilitated. The inability to sense a stress-inducing change in the environment is most likely to occur when the change is novel, i.e., one which bears little similarity to past events (Slobodkin & Rapoport, 1974).

Either behavioral or neurophysiological techniques may be used to establish sensitivity, depending upon the specific question to be answered. In this work we have used behavioral criteria exclusively because they have proven to be quite effective for determining sensitivity to various substances. For example, utilizing changes in the rate of antennule flicking and gill bailing, Pearson and Olla (1977) showed the threshold concentration at which blue crabs, Callinectes sapidus, detected a food extract to be 10^{-12} mg/L. Blue crabs were also able to detect naphthalene (Pearson & Olla, 1979) at a threshold concentration of 10^{-7} mg/L (Pearson & Olla, 1980) and the water-soluble fraction (WSF) of crude oil at 10^{-6} mg/L (Pearson et al., 1980a).

While detection may occur at very low concentrations, the elicitation of more complex behaviors appears to require much higher concentrations. In the blue crab, food searching did not occur until the concentration of a food extract reached 10 mg/L, 13 orders of magnitude higher than the detection level (Pearson & Olla, 1977). When presented with naphthalene, the blue crab showed active locomotory behavior at a concentration of 2 mg/L, about 7 orders of magnitude higher than the detection level (Pearson & Olla, 1980).

For the Dungeness crab we used techniques similar to those we had with the blue crab to ask whether and at what concentration the Dungeness crab detected petroleum hydrocarbons. Detection of petroleum hydrocarbons is the first step to behavioral mitigation of their effects. The following

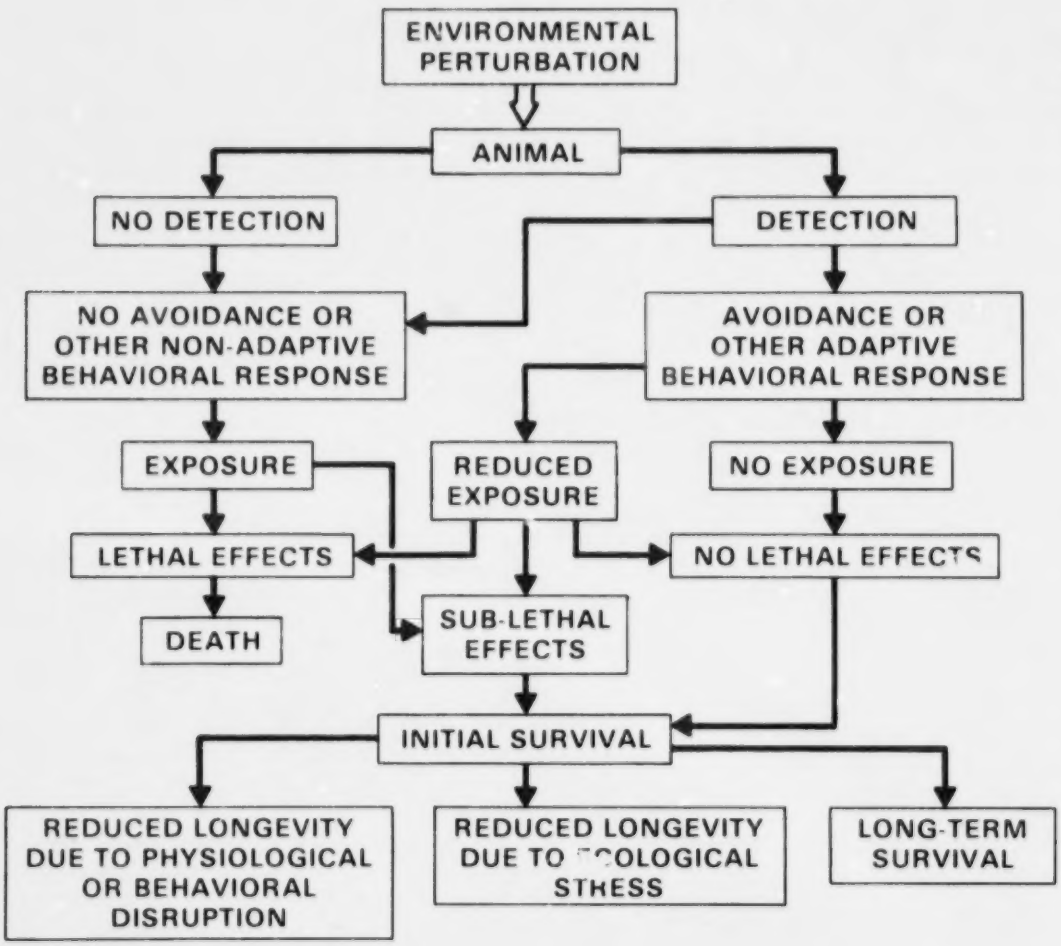

Figure 1. A flow-chart indicating possible behavioral responses to an environmental perturbation and their consequences.

From Olla et al., 1980a.

A. Detection of Petroleum Hydrocarbons by the Dungeness Crab, Cancer magister.

For decapod crustaceans the antennules have been considered the site of distance chemoreception (Hazlett, 1971a), and their flicking may be analogous to sniffing in vertebrates (Fuzessery, 1978). Previous work has shown that in the blue crab, Callinectes sapidus, the antennular behavior indicating detection of food substances (Pearson & Olla, 1977) also indicated detection of the petroleum hydrocarbon naphthalene (Pearson & Olla, 1979, 1980) and the water soluble fraction of crude oil (Pearson et al., 1980a). In the Dungeness crab, similar antennular behavior, i.e., a change in orientation and increased flicking rate, also indicated detection of food substances (Pearson et al., 1979). Here we used these changes in antennular behavior to determine chemosensory detection thresholds in the Dungeness crab for naphthalene and the water soluble fraction (WSF) of Prudhoe Bay crude oil.

Materials and Methods --

Dungeness crabs trapped in the Strait of Juan de Fuca, Washington, were held outdoors in 1200-liter tanks under the conditions described by Pearson et al. (1979). The seawater temperatures during the naphthalene and WSF experiments were 12.7 (± 0.6 SD)°C and 10.6 (± 0.3)°C; the salinities, 31.6 (± 0.9) °/$_{oo}$ and 32.0 (± 0.0)°/$_{oo}$; the dissolved oxygen, 6.9 (±0.7) mg/L and 7.3 (± 0.5) mg/L; and the pH, 8.12 (± 0.17) and 8.02 (±0.16), respectively.

Experimental Solutions -- Saturated solutions of naphthalene were prepared by adding naphthalene crystals to seawater filtered through a 0.4 µm Nucleopore membrane. These stock solutions were stirred continuously at room temperature on a magnetic stirrer and were used after at least 18 h of stirring and no more than five days from first use. On each day of testing, a portion of the stock solution was siphoned off and passed through a 100 mL glass syringe fitted with a Millipore prefilter (Type AO25) to remove any naphthalene crystals. Less than one hour before testing, serial dilutions of this filtered stock naphthalene solution were made with seawater freshly filtered through a 0.4µm membrane. An aliquot of the filtered seawater used for dilution served as the control solution. Experimental and control solutions were kept in a water bath at ambient sea-water temperature during testing.

On each day of testing, samples of the stock solution and 10^{-1} dilution were analyzed for naphthalene content. Ten milliliters of hexane were vigorously shaken with 50 mL of sample solution for one minute. This hexane was removed and analyzed for napthalene content by capillary GC methods (Bean et al., 1978). The stock naphthalene solution was 22.9 (± 2.1) mg/L, and the 10^{-1} dilution was 2.2 (± 0.2) mg/L.

The water soluble fraction (WSF) of Prudhoe Bay crude oil was prepared freshly each day by methods similar to Anderson et al. (1974). In a 19-liter glass bottle, one part oil was gently poured over nine parts membrane-filtered seawater. Before the oil was added, a glass siphon tube inserted through a stopper covered with aluminum foil was placed in the filtered seawater. With the bottle stoppered, the seawater was slowly stirred on a magnetic stirrer for 20 h at room temperature. The stirring speed was adjusted so

that the vortex did not extend more than 25% of the distance to the bottom of the bottle. After mixing, the oil and water phases were allowed to separate for one hour. The water phase was then siphoned from below the oil phase and filtered through a prefilter under very low pressure to remove any remaining oil droplets. Serial dilutions of the resulting WSF were then immediately made with freshly membrane-filtered seawater and kept in a water bath at ambient seawater temperature during use. The membrane-filtered seawater used for dilution was the control solution. The stock WSF was analyzed by capillary gas chromatography for di- and tri-aromatic hydrocarbons (Bean et al., 1978), and by gas partitioning analysis modified from McAuliffe (1971) for monoaromatics.

Chemosensory Threshold Determination -- The apparatus and procedures of Pearson et al. (1979) were used here. In brief, glass testing chambers were arranged on four trays, 10 chambers to a tray, and the trays were surrounded by blinds. The experimental solutions were introduced into each testing chamber through an inlet manifold connected to a glass funnel. Seawater from dripper arms entered each funnel at a rate of 1.0 L/min. A teflon delivery tube carried the experimental solutions to the funnel from a buret calibrated to deliver 20 mL in 15 s.

To obtain a dilution factor for estimating the effective concentration of experimental solutions within a testing chamber, seawater solutions of ^{14}C-naphthalene (sp. act. 3.6 mCi/mmole, Amersham-Searle Corporation) were introduced and samples taken at timed intervals from the midpoint of the chamber and counted for radioactivity by liquid scintillation spectrometry. The chamber contained a crab model displacing 701 mL, a volume typical of the crabs tested. The maximum concentration in the chamber occurred 45 s after ^{14}C-naphthalene was added and was 0.0188 (± 0.0058 SD) times the concentration of the introduced solution. This dilution factor did not differ significantly from that found by Pearson et al. (1979) using a visible dye.

Approximately 24 h before testing, crabs were transferred to the testing chambers from the holding tanks where they had been fed an ad libitum diet of blue mussels, Mytilus edulis. Because, in preliminary experiments, tidal phase was found to influence chemosensory responses (Pearson et al., 1979), testing was synchronized to begin and end within either a rising or falling tide. The seawater for the test dilutions and control was drawn and filtered one hour after a tidal change. Testing then began as soon as possible and stopped before the next tidal change.

Each day a maximum of 40 crabs were presented individually with 20 mL of either one of nine dilutions of naphthalene stock solution, one of eight dilutions of WSF, or a control of filtered seawater. Molting and mating crabs were not tested. The order in which individual crabs were watched and the choice of experimental solution were randomized except that active crabs and ones with retracted antennules were passed over. The observer did not know the identity of any test solution. Individual crabs were observed for 1.0 min prior to introduction of the experimental solution, and their antennular flicking rate and other behavior recorded. The flicking rate of one antennule was measured using a hand-held counter. The solution was then introduced, and the observations continued for 1.0 min after the beginning of solution addition. The behavior was scored with the criteria used by Pearson et al. (1979).

To be scored as detecting an experimental solution, a crab had to exhibit an abrupt change in the orientation of the antennules within 30 s after solution introduction, and the ratio of the antennular flicking rate for 1.0 min after solution introduction to that for 1.0 min before had to be 1.50 or above. This value was determined previously by Pearson et al. (1979) from observations of crabs in the testing apparatus without any solutions present. Because 1.50 was the 95th percentile of these antennular flicking rate ratios, the a priori probability that a flicking rate ratio greater than 1.50 represented a spontaneous increase rather than a reaction to the experimental solution was less than 5%.

Results --

Composition of the WSF -- The monoaromatic hydrocarbons by far dominated the WSF (Table 1.) and comprised 99.1% of the total hydrocarbons measured. The remaining aromatic hydrocarbons, mostly the naphthalenes, were present at concentrations 100 times less than that of the monoaromatics. The hydrocarbons partitioned into the WSF from the crude oil in proportion to their solubility in seawater (Clark & MacLeod, 1977; Bean et al., 1978).

Detection Thresholds -- Dungeness crabs detected both naphthalene and the water soluble fraction (WSF) of Prudhoe Bay crude oil, with the complex mixture (WSF) being more readily and consistently detected. Because the percentage of crabs detecting naphthalene varied widely over the range of concentrations presented, the regression equation relating percentage detection and the logarithm of concentration was not significant ($F = 1.3$, $P = 0.30$) (Fig. 2). The curve for naphthalene detection was sawtooth-shaped with the percentage of detection being high at 10^{-8} mg/L and approaching control valves at other concentrations. Above 10^{-6} mg/L, however, the percentage of crabs detecting naphthalene rose linearly with concentration and the regression equation was significant ($F = 29.1$; $P = 0.01$) and of low variability ($R^2 = 94\%$). The threshold concentration at which 50% of the crabs detected naphthalene, calculated from this latter regression equation, was 3×10^{-2} mg/L. In contrast to naphthalene, the percentage of crabs detecting the WSF decreased in a consistent way with the WSF concentration (Fig. 2). The regression equation was significant ($F = 60.4$, $P << 0.01$), and the variability was low ($R^2 = 91.0\%$). The 50% detection threshold was 4×10^{-4} mg/L, about 100 times lower than that for naphthalene.

When a crab detected naphthalene or WSF, the response was usually distinct. For crabs meeting the detection criteria, the median ratios of the antennular flicking rates did not vary with concentration (Median Tests, $\chi^2 = 2.38$, $P = 0.12$ for naphthalene; $\chi^2 = 9.07$, $P = 0.75$ for WSF), so that what varied with concentration was the percentage of crabs responding and not the magnitude of the response. Also, the magnitudes of the increase in antennular flicking were the same for both naphthalene and WSF. For naphthalene, the grand median of the antennular flicking rate ratios was 2.04; for the WSF, the grand median was 1.96.

Table 1. The composition of the WSF of Prudhoe Bay crude oil. Sample size was 3 for the di- and triaromatics and 6 for the mono-aromatics.

	mg/L
TOTAL ALKANES	< 0.001
NAPHTHALENE	0.0851 ± 0.0088
TOTAL METHYLNAPHTHALENES	0.0766 ± 0.0080
TOTAL DIMETHYLNAPHTHALENES	0.0269 ± 0.0015
PHENANTHRENE	0.0006 ± 0.0004
METHYLPHENANTHRENE	< 0.0001
DIMETHYLPHENANTHRENE	< 0.0001
TOTAL POLYNUCLEAR AROMATICS	0.1892 ± 0.0175
BENZENE	10.00 ± 0.29
TOLUENE	6.74 ± 0.42
ETHYLBENZENE	0.30 ± 0.02
m + ρ XYLENE	1.12 ± 0.06
o-XYLENE	1.12 ± 0.08
TOTAL TRIMETHYL BENZENES	0.46 ± 0.12
TOTAL MONOAROMATICS	19.75 ± 0.86
TOTAL HC MEASURED	19.94

From Pearson et al., 1980b.

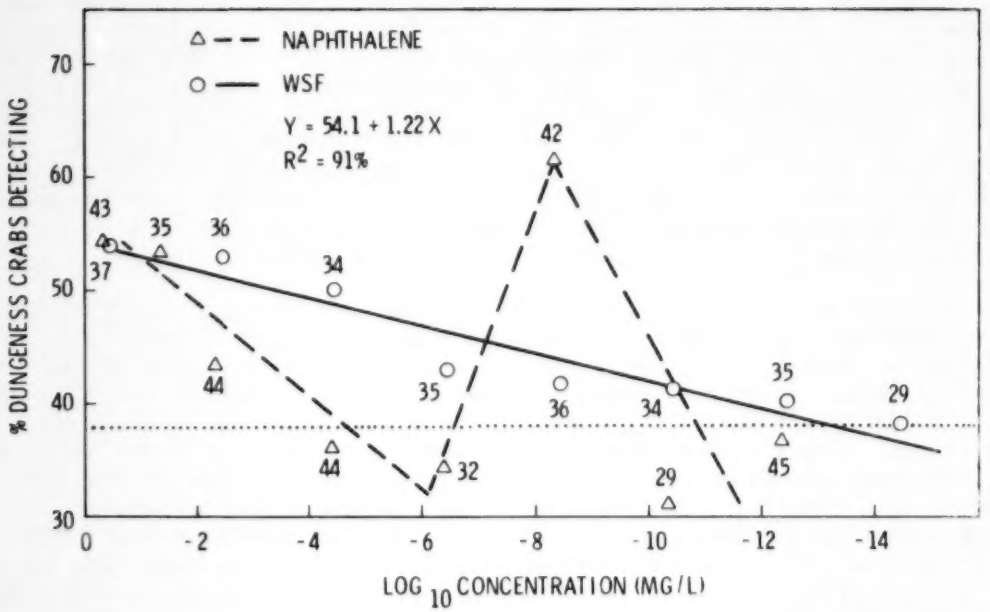

Figure 2. The percentage of Dungeness crabs detecting naphthalene and the water soluble fraction (WSF) of crude oil as a function of the logarithm of concentration (mg/L). The percentage of crabs detecting a control of membrane-filtered seawater was 28.8% (n = 66) for naphthalene and 26.8% (n = 41) for WSF. The number beside each point is the number of trials at the concentration.

From Pearson et al., 1980b.

Discussion --

When presented with naphthalene or WSF of crude oil, Dungeness crabs, Cancer magister, changed antennular orientation and flicking rate in the same manner as when presented with a clam extract. The blue crab, Callinectes sapidus, also gives the same detection behaviors for hydrocarbons as for food (Pearson & Olla 1977, 1979, 1980; Pearson et al., 1980a), and the similar findings in both species indicate that chemoreception by these crustaceans is not restricted to chemical cues for food and, thus, agree with Ache's (1975) suggestion that the chemical spectrum sensed by decapod crustaceans is really quite broad.

While the manner of antennular response to naphthalene and WSF was the same as that to a clam extract, the magnitudes of the flicking increase were slightly less and the chemosensory thresholds were 10^5 and 10^3 times higher than those found for the clam extract (Pearson et al., 1979). The grand median ratios of flicking rates for naphthalene and WSF, 2.04 and 1.96, respectively, were lower than that for the clam extract, 2.67. Also, the ranges of flicking ratios for the hydrocarbons were less than 30% of that for the clam extract. The slightly less intense response and much higher thresholds suggest that the petroleum hydrocarbons rank as much less potent chemical cues than sapid chemicals from a natural food.

Previously, Pearson and Olla (1980) had hypothesized that the chemical and chemosensory processes producing a higher detection threshold for a single petroleum hydrocarbon, naphthalene, than for a complex mixture of hydrocarbons, the WSF of crude oil, are analogous to the processes producing a similar relationship of thresholds for single amino acids and complex mixtures. Usually, food extracts and complex mixtures of amino acids and other chemicals have a lower detection threshold than that of a single amino acid (Mackie, 1973; McLeese, 1974). Indeed, with the Dungeness crab the detection threshold for WSF was two orders of magnitude lower than that for naphthalene. Also, the variability in detection was much less for WSF than for naphthalene. This apparent greater difficulty in detecting the single hydrocarbon than the more complex WSF is presumptive evidence for the hypothesized analogy. With naphthalene constituting only 0.4% of the total hydrocarbons in the WSF, the crabs were probably responding primarily to other compounds or, perhaps, to some sort of odor medley.

One possible explanation for the extreme variability in naphthalene detection is that detection at high naphthalene concentrations was inhibited by some toxic, narcotic, or anesthetic action not present or much reduced at low concentrations. The blocking of chemosensory feeding and mating responses in the crab, Pachygrapsus crassipes, after 24-h exposure to naphthalene at 10^{-3} mg/L (Takahashi & Kittredge, 1973) supports the possibility of such inhibition. If the threshold concentration for chemosensory inhibition was within the range of concentrations we presented, then a sharp increase in the percentage of crabs detecting naphthalene would be expected below the inhibition threshold and would produce the sawtooth-shaped curve seen for naphthalene in Figure 2. A sawtooth-shaped curve would also result if the sensitive antennular chemoreceptors were more impaired than the less sensitive body chemoreceptors on the dactyls, chelae, and mouthparts. If so, detection would occur mainly through the body chemoreceptors at high naphthalene levels and would switch to the antennules at low levels below

the relatively high detection threshold of the body chemoreceptors and where any inhibitory effects of the naphthalene on the antennules were lessened.

For both food extract and petroleum hydrocarbons, the blue crab has exhibited more acute chemoreception than the Dungeness crab (Pearson & Olla, 1977, 1979, 1980; Pearson et al., 1980a). Pearson et al. (1979) hypothesized that the lower detection threshold for clam extract seen in the blue crab was a consequence of the blue crab's greater ability to sample the chemical environment with its higher flicking rate and larger antennules. This hypothesis would apply equally to the differences between the two crabs in the hydrocarbon detection thresholds.

An important practical question is how the ability of the Dungeness crab to detect petroleum hydrocarbons compares with the range of hydrocarbon concentrations likely to be encountered by the crab. In the water column during an oil spill, McAuliffe et al. (1975) found concentrations of dissolved hydrocarbons ranging from 2×10^{-3} to 2×10^{-1} mg/L. Of these dissolved hydrocarbons about one half were the monoaromatics dominating the WSF used here. During a spill from a North Sea platform, Grahl-Nielson (1978) found petroleum hydrocarbon concentrations ranging up to 4×10^{-1} mg/L. In the open sea between Nova Scotia and Bermuda, Gordon et al. (1974) found petroleum hydrocarbon concentrations of 2.04×10^{-2}, 8×10^{-4}, and 4×10^{-4} mg/L at the surface, 1 m and 5 m, respectively. These concentrations roughly agree with those given for relatively uncontaminated oceanic areas by Clark and MacLeod (1977), who also stated that chronically contaminated areas have hydrocarbon concentrations about two orders of magnitude higher than those of the open sea. Unfortunately, analytical difficulties in distinguishing petrogenic from biogenic hydrocarbons at low environmental concentrations make estimates of oil levels in chronically contaminated areas uncertain. For the North Sea, Grahl-Nielsen et al. (1979) found that despite considerable oil production there was no apparent standing crop of petroleum hydrocarbons, but rather petroleum contamination occurred as localized, transient patches. Thus, the petroleum hydrocarbon concentrations in uncontaminated (10^{-4} to 10^{-3} mg/L), chronically contaminated (10^{-4} to 10^{-2} mg/L), and oil spill (10^{-3} to 10^{-1} mg/L) situations are all at or above the WSF detection threshold (10^{-4} mg/L) so that Dungeness crabs can detect hydrocarbons readily at the concentrations found in oil spill situations, probably in chronically contaminated situations, and marginally in uncontaminated situations. In being able to detect the petroleum hydrocarbons at concentrations at and below those found in oil spill situations, Dungeness crabs can achieve the first step to any subsequent behavioral response to petroleum.

B. Avoidance of Oiled Sediment by the Dungeness Crab, Cancer magister.

Our next series of experiments examined whether the crab could change its behavior to eliminate or reduce petroleum exposure, and this section presents work in preparation for submission for publication by Pearson, Sugarman, Woodruff, Blaylock and Olla.

Whether crabs could avoid contaminated sand was considered the ecologically relevant question because sandy bottoms are an important environmental resource for the Dungeness crab. Their importance is indicated by

the considerable extent to which crabs bury in the sand during their daily activity cycle (Pearson et al., 1979) and by the high degree to which the crab's diet consists of animals, e.g., clams, that are buried in sandy substrates (Butler, 1954; Gotshall, 1977). In addition, some sandy bottoms may be more suitable than others for various life habits. For example, our field observations indicated that crabs were burying in distinct patches of sand where the shear force of sediment took a very narrow value compared to the range of penetrability found in the general area.

Because of the importance of the sandy bottoms to Dungeness crabs, the long-term effects of an oil spill may derive not from oil-contaminated water, but from contact with oiled sediment. Krebs and Burns (1977) presented evidence that at least seven years after the West Falmouth Oil Spill contact with oiled sediment was still producing behavioral abnormalities and reduced population densities in the fiddler crab, Uca pugnax. Because the Dungeness crab may be similarly vulnerable, the experiments reported here examined the ability of the crab to avoid oiled sediment. Ecological consequences from either avoidance or failure to avoid can be expected. Avoidance probably denies the crab a patch of important resources whereas failure to avoid could lead to adverse effects deriving from oil exposure.

Our field observations of the behavioral response of crabs to plumes of freshwater during high runoff produced a preliminary hypothesis concerning one possible behavioral response to oiled sediment that might occur. When freshwater plumes were present Dungeness crabs left the eelgrass beds and moved deeper with the downstream current to bury in the sand. Some preliminary experiments suggested that a downstream movement, followed by burying, may also occur with oiled sediment. A portion of the experiments reported here addressed this question.

We performed a series of replicate experiments. The initial experiments compared crab behavior in large partitioned and unpartitioned tanks to see whether the tendency of crabs to bury downstream influenced the avoidance of oiled sand. The next experiments examined how the oil-in-sand concentration influenced avoidance. The last experiments concerned how weathering of the oil might change avoidance behavior.

Materials and Methods --

The general approach in determining the occurrence and extent of oiled sediment avoidance was to place Dungeness crabs in large tanks with oiled and clean sediment and then observe the time spent in various clean and oiled areas. Both partitioned and unpartitioned tanks were used to examine whether avoidance behavior would differ if the crab's downstream movement did not permit avoidance of oiled sediment. Table 2 gives some of the parameters of the experiments reported here.

Animal Collection and Maintenance -- Dungeness crabs, Cancer magister, were trapped in the Strait of Juan de Fuca, Washington, and held outdoors in eight 1200-liter tanks. Molting and mating crabs were isolated from those to be tested. Seawater drawn from the entrance of Sequim Bay entered each holding tank through a manifold under a 15-cm layer of gravel and sand. The crabs readily buried in the sand. Carapace size of crabs used in the various experiments is given in Table 2. Individual crabs were marked with variously shaped pieces of flat, white teflon secured with stainless steel wire wrapped about the carapace.

Experimental Tanks -- The experimental tanks were 2.4 x 1.2 x 0.6 m and constructed of 1.2-cm plywood coated with finishing type fiberglass resin. A continuous flow of filtered sea water entered each tank at 5 L/min at the midpoint behind a fiberglass baffle that extended across the entire tank width. Holes were drilled on a 2.5 cm square grid across the entire baffle. Hole sizes increased from the midpoint of baffle to each side and were adjusted to promote an even cross-sectional flow from one end of the tank to the other. An identical baffle was positioned at the downstream end of the tank 5 cm from a solid fiberglass end plate. After passing through the downstream baffle, seawater spilled over this 47-cm high end plate into a drain. Sediment depth was 7 cm and oiled and unoiled sediment were separated by a barrier extending from bottom of the tank to the top of the sediment.

Both unpartitioned and partitioned tanks had oiled sediment covering the same surface area but in different positions relative to water flow. Unpartitioned tanks had the downstream one-half covered with either clean or oiled sand. The upstream end always had clean sand. A crab could walk in a straight line from any position in the tank to any other. Partitioned tanks had a solid fiberglass sheet running down the middle for three quarters the length of the tank. The whole length of the tank was covered with clean or oiled sediment on one side and with clean sand on the other. A crab could move into or out of the oiled sediment only on the downstream one quarter.

Preparation of Oiled Sediment -- Sand was mixed with Prudhoe Bay crude oil for addition to the experimental tanks. The sand was washed over a 0.32 mm mesh Nitex screen to remove the fine silts. The resulting geometric mean size was 1.2 mm.

To produce oiled sand with nominal concentrations of 10000 ppm, 1000 ppm, and 100 ppm, 135 L of coarse washed sand was mixed to 1350 mL, 135 mL, and 13.5 mL of Prudhoe Bay crude oil, respectively, in a cement mixer for 30 min. Equal amounts of oil and seawater were stirred in a high speed blender for 30 sec before being mixed into the sand. The minimum of additional seawater necessary to yield a smoothly flowing mixture was added to the cement mixer. During the addition of the oiled sand to the tanks and introduction of seawater, the oil concentrations were expected to fall to between 10 and 20% of the nominal value. Such reduction would have produced oil concentrations typical of polluted sediment (Clark & MacLeod, 1977).

The actual oil concentrations in the sediment were determined from composite core samples taken at the beginning of the first and end of each subsequent experiment. Each composite consisted of 5 sediment cores (7 cm x 2.5 cm diameter). Three composite samples were taken from each control tank and three were drawn from each half of the oiled tanks. Total oil levels were measured by infrared spectrophotometry (Simard et al., 1951; Anderson et al., 1979).

Oil concentrations in the water column were determined from 50 mL water samples drawn from the midpoint of the downstream end of the partitioned oiled tanks in about 15 cm above the oiled sand. Samples were drawn twice daily 12 hours apart. To test the oil distribution within a tank, samples were drawn from the ends and center of each side. The hydrocarbon concentration and components were analyzed by helium equilibration gas chromatography (Bean & Blaylock, 1977).

Procedure -- Forty-eight hours after the oiled sand had stood in running seawater, 6 crabs were added to each tank in the middle of the upstream end. Observations began one hour later and were taken hourly for the duration of the experiments. The activity and position, by quadrant, of the crabs were observed and recorded on a data sheet for each tank. The activities assigned relative values and recorded by shorthand codes were: ACTIVE - walking (2), climbing (2), standing (1); INACTIVE - resting (0), and buried (-1). Behavior scores were tallied hourly for each tank and the behaviors by quadrant were summed daily.

Ambient tidal levels were monitored hourly with a Metercraft tide chart recorder (Style No. 80-H).

For the weathering experiment all crabs were removed from all tanks after the first 5-d observation period. After the tanks had stood for another 2 d, a new group of crabs were introduced and observed for 3 d after they were in turn removed. After 8 weeks, another group of crabs were introduced and observed for 3 d. Clean seawater entered the tanks continuously whether crabs were present or not.

Results --

In the unpartitioned tanks Dungeness crabs generally avoided oiled sand. In the control tanks crabs spent more time downstream than upstream, but in the tanks with oiled sand downstream significantly decreased time was spent downstream (Table 3).

The measured concentration of oil in the sand fell during the experiments (Table 4). During the first five days that crabs were present, oil concentrations fell about 20%. As the crabs buried themselves in the oiled sand, we observed droplets of oil floating up through the water column. After two months with a total of 11 days during which crabs were present, oil concentrations were about half of the initial concentration. The loss of oil then was probably heavily influenced by the activity level of the crabs. Indeed the monoaromatic content of the water column often reached its highest levels (up to 297 ppb) during periods of high activity. Great amounts of monoaromatic hydrocarbons were found only over the highly oiled sand (Table 5).

In the partitioned tanks crabs avoided oiled sand but not under all circumstances. In control tanks crabs did not spend more time on one side than the other, but in tanks with oiled sand on one side, crabs spent less time on highly oiled sand and more time on oiled sand of moderate and low concentration than on clean sand (Table 6). For only the time spent inactive, i.e., buried in or resting on sand, the same pattern emerges (Table 7). In this case the crabs spent 70% of the inactive time either buried in or resting on the moderately oiled sand.

Analysis of variance indicated a significant variation with the oil concentration but no significant weathering or interaction effects. Nonetheless, after two months crabs on the highly oiled sand were apparently no longer spending less time on oiled sand while crabs on the lowly and moderately oiled sand continued to spend more time on oiled than clean sand.

We could not detect any changes in the overall activity level of the crabs due to oiled sand (Table 8). Activity levels did vary from experiment to experiment, but this variation was apparently related to the tidal cycle prevailing at the time of the experiment. The crabs were generally active at night but inactive, i.e., buried and resting, during the day. During an extreme low tide during the night or in extreme high tide during the day, crabs tended to decrease activity while during a large change in tidal height crabs increased activity. How the tidal cycle interacted with the day-night cycle apparently determined the level and pattern of activity.

Table 2. Experimental conditions in experiments concerning avoidance of oiled sand.

TEST	DATES	CRAB SIZE $\bar{x} \pm SD$ cm (n = 48)[a]	TEMPERATURE $\bar{x} \pm SD$ °C (n = 3)	SALINITY $\bar{x} \pm$ °/oo (n=3)	D.O. $\bar{x} \pm SD$ mg/L (n=3)	NO. REPLICATES/TREATMENT Control		Oil			
						Unpart.	*Part.*	*100*	*1000*	*10000*	*10000 Unpart*
I	12/17 - 12/22/78	N.D.[b]	7.0 ± .2	32.0	8.6 ± .2	1	1			1	1
II	5/6 - 5/11/79	15.2 ± 1.2	11.2 ± .4	32.0	7.4 ± .4	2	2			2	2
III	9/30 - 10/5/79	15.1 ± .7	10.1 ± .2	32.0	7.8 ± .3	2	2			2	2
IV	1/28 - 2/2/79	15.5 ± .7	6.3 ± 2	32.0	8.4 ± .2		1	1	1	1	
VA	10/21 - 10/26/79	15.9 ± 1.4	10.1 ± .2	32.0	6.9 ± .7		2	2	2	2	
VIA	12/9 - 12/14/79	15.7 ± .7	9.5 ± .1	32.0	N.D.		2	2	2	2	
VB[c]	10/30 - 11/2/79	16.1 ± .8	10.1 ± .1	32.0	7.9 ± .3		2	2	2	2	
VIB[c]	12/18 - 12/21/79	15.6 ± .6	8.7 ± .1	32.0	N.D.		2	2	2	2	
VIC[d]	2/4 - 2/7/80	16.4 ± 1.1	6.9 ± .1	31.0	8.1 ± .2		2	2	2	2	

[a] Except for I and II where n = 24
[b] N.D. = not determined
[c] Oil weathered in experimental apparatus 1 week
[d] Oil weathered in experimental apparatus 8 weeks

Table 3. Time spent by Dungeness crabs in clean and oiled sand in the unpartitioned tanks. Initially the oil-in-sand concentration was 2882 (±854) ppm; at the end, 2315 (±496) ppm. Results from 5 replicate tanks are pooled for each treatment.

		NUMBER OF CRAB HOURS OBSERVED		
		UPSTREAM	DOWNSTREAM	
CONTROL				
	Buried & Resting	849	1494	(63.8%)[a]
	Total	1470	2130	(59.2%)[b]
OILED				
	Buried & Resting	1108	948	(46.1%)[a]
	Total	1935	1665	(46.2%)[b]

[a] Oiled differs significantly from control, $X^2 = 138.2$; $p > 0.999$
[b] Oiled differs significantly from control, $X^2 = 120.5$; $p > 0.999$

Table 4. Oil-in-sand concentrations in partitioned tanks determined by IR spectrophotometry.

TIME	OIL CONCENTRATION (ppm) IN SAND			
	CONTROL	LOW	MODERATE	HIGH
First Week				
Beginning	5.1 ± 1.8	16.2 ± 4.4	192 ± 71	2508 ± 978
End	4.1 ± 0.4	17.8 ± 5.5	146 ± 39	2021 ± 686
Second Week				
Beginning	4.4 ± 0.7	16.8 ± 5.7	160 ± 27	1788 ± 406
End	4.5 ± 1.0	10.0 ± 2.8	141 ± 65	1281 ± 223
At Two Months				
Beginning	4.0 ± 0	8.0 ± 0	85 ± 10	1222 ± 4
End	6.0 ± 2.8	7.0 ± 4.2	72 ± 4	1381 ± 16

Table 5. Total concentrations of monoaromatic hydrocarbons in partitioned tanks determined by helium equilibration gas chromatography. (The number of samples is enclosed in parentheses.)

	TOTAL MONOAROMATIC CONCENTRATION (ppb)					
	LOW		MODERATE		HIGH	
FIRST WEEK	(20)	0.2 ± 0.9	(20)	0.4 ± 1.3	(40)	45.8 ± 62.3
SECOND WEEK	(4)	2.1 ± 3.4	(4)	0.7 ± 0.5	(8)	9.2 ± 8.7
THIRD WEEK		N.D.		N.D.	(8)	4.3 ± 3.6

Table 6. Average percentages of the total crab-hours observed in partitioned tanks that Dungeness crab spent in oiled sand. The left half of the tanks was used for control. (The number in parentheses is the number of replicate tanks.)

	PERCENTAGE OF TIME SPENT ON OILED SAND			
	Control	Low	Moderate	High
FIRST WEEK	52 (10)	51 (5)	58 (5)	42 (10)
SECOND WEEK	56 (4)	58 (4)	58 (4)	40 (4)
AFTER TWO MONTHS	41 (2)	57 (2)	66 (2)	55 (2)
OVERALL	50	55	61	46

Table 7. Average percentages of the crab-hours observed in partitioned tanks buried and resting that Dungeness crabs spent buried and resting in oiled sand. For controls the left side of the tank was used to calculate the percentage. (The number of replicate tanks is enclosed in parentheses.)

	PERCENTAGE OF INACTIVE TIME SPENT INACTIVE IN OIL			
	Control	Low	Moderate	High
FIRST WEEK	51 (10)	55 (5)	67 (5)	41 (10)
SECOND WEEK	58 (4)	60 (4)	67 (4)	31 (4)
AFTER TWO MONTHS	38 (2)	58 (2)	76 (2)	54 (2)
OVERALL	49	58	70	42

Table 8. Average percentages of total crab-hours observed in partitioned tanks that Dungeness crabs were active.

	PERCENTAGE OF TIME ACTIVE			
	Control x S.D.	Low x S.D.	Moderate x S.D.	High x S.D.
FIRST WEEK	46 ± 22	52 ± 16	57 ± 15	43 ± 9
SECOND WEEK	52 ± 4	59 ± 6	65 ± 10	56 ± 4
THIRD WEEK	46 ± 20	48 ± 1	43 ± 0	50 ± 3

Discussion --

Before detailed discussion is possible, more analysis of the data only briefly presented here is necessary. Nonetheless, several trends are emerging.

Dungeness crabs avoid oiled sand, but not under all circumstances. There was not a threshold oil concentration above which the crabs avoided oiled sand and below which they were indifferent to it. Oiled sand with 1000 to 2000 ppm was avoided but sand with less than 200 ppm attracted crabs.

Although no significant weathering effects were found, the number of replicates at two months was low. Quite possibly a longer experiment with more replication would detect a weathering effect.

While any effects of oiled sand on the level or pattern of activity was not obvious, the variation in the activity levels and patterns indicates a need to consider seasonal changes in behavior in designing and interpreting experiments such as these. Seasonal variation in activity could well have contributed to the observed high variability in the extent of avoidance.

Factors characteristic of the animal, the petroleum, and the environment all interact in determining the occurrence and extent of avoidance of oiled sand. Taken as a whole, these experiments indicate that avoidance of oiled sediment is more than a possibility but not a certainty, and, therefore, the need exists to understand both the circumstances that favor or preclude avoidance and the effects of exposure to oiled sand when avoidance is less than complete.

II. BEHAVIORAL EFFECTS OF PETROLEUM EXPOSURE

Because successful behavioral mitigation of exposure effects was not assured under all circumstances, we examined the effects of petroleum exposure on the chemosensory-directed feeding behavior of the Dungeness crab. Chemoreception was chosen because chemoreception is the primary sense in many life habits of marine organisms (Grant & Mackie, 1974) and because ecologically important behavorial effects from petroleum would most likely derive from disruption of chemoreception and the associated behaviors (Blumer, 1969; Takahashi & Kittredge, 1973; Olla & Samet, 1974). We took three steps on this pathway, establishing a baseline for sensitivity to chemical food cues, examining whether such sensitivity changed under petroleum exposure and studying how well crabs could find prey buried in oiled sand. These steps are described in the following sections.

Section II.A. is work already published by Pearson, Sugarman, Woodruff, and Olla (1979) in the Journal of Experimental Marine Biology and Ecology and describes the high sensitivity of Dungeness crabs to chemical food cues. Section II.B., a manuscript submitted for publication, shows how a 24-h exposure to water contaminated with crude oil at concentrations typical of an oil spill impaired the distance chemoreception seated in the crab's antennules. Section II. C., another manuscript ready for submission, describes how we examined the ability of Dungeness crabs to find and take clams buried in oiled sand. Due to a change in the clam's burrowing behavior that increased its accessibility, crabs consumed more clams from oiled than clean sand. Thus, a behavioral change tending to mitigate exposure led the clam into vulnerability to ecological stressors. We indicated this possibility in our theoretical schematic (Figure 1).

A. Thresholds for Detection and Feeding Behavior in the Dungeness Crab, Cancer magister.

Chemoreception is a sensory modality important to many life habits in marine organisms (Grant & Mackie, 1974). A necessary step towards understanding the relation between chemoreception and ecology is to determine the chemosensory acuity or threshold of an organism for particular chemical signals (Wilson, 1970). Commonly, feeding responses have been used as behavioral criteria for determining chemosensory abilities in crustaceans (McLeese, 1970, 1974; Mackie & Shelton, 1972; Mackie, 1973; Fuzessery & Childress, 1975), but Pearson and Olla (1977) have suggested that overt feeding responses may not be the most sensitive behavioral indicators of chemical detection by crustaceans. By observing changes in antennular flicking and gill bailing, they found that the threshold concentration at which the blue crab, Callinectes sapidus, detected a food extract was 10^{-15} g/L which was many orders of magnitude below the concentration at which chelae probing began. Here we report chemosensory thresholds for the Dungeness crab, Cancer magister (Dana), also determined through measurement of changes in antennular movement.

Despite the demonstrated importance of the antennules to chemoreception, antennular movements have been sparsely studied and hardly ever used to

measure chemosensory thresholds. The antennules of decapod crustaceans have been shown to be the distance chemoreceptors involved in feeding behavior (Hazlett, 1971a), orientation to odors (McLeese, 1973), sex recognition (Ameyaw-Akumfi & Hazlett, 1975), host location (Ache, 1975) and sex pheromone reception (Christofferson, 1970, 1972). Although crustacean antennules have been the subject of considerable electrophysiological investigation (Levandowsky & Hodgson, 1965; Van Weel & Christofferson, 1966; Ache & Case, 1969; Ache, 1972; Shepheard, 1974; Fuzessery & Childress, 1975; Ache et al., 1976; Price & Ache, 1977; Fuzessery, 1978; Fuzessery et al., 1978), antennular behavior in whole animals has been rarely studied. Snow (1973) described antennular activities in the hermit crab, Pagurus alaskensis, and discussed the factors influencing flicking rate. In an attempt to develop artificial bait for the Dungeness crab, Allen et al. (1975) have used changes in antennule orientation as one measure among several to score the intensity of feeding responses to various natural and artificial substances. Antennular flicking may facilitate chemoreception, and increased flicking rates in the presence of sapid chemicals have been reported for Homarus gammarus (Mackie & Shelton, 1972), Pleuroncodes planipes, Cancer antennarius, Spirontocaris taylori, Pagurus hirsutiusculus (Fuzessery & Childress, 1975) and Panulirus argus (Price & Ache, 1977). Only Pearson and Olla (1977) have explicitly used antennular flicking rates as the basis for measuring chemosensory acuity.

After observation of the behavior of Dungeness crabs in laboratory and field, the threshold concentrations at which crabs detected a food extract and exhibited feeding behavior were measured. To facilitate interspecific comparison we used experimental apparatus and procedures similar to those previously used for the blue crab (Pearson & Olla, 1977).

Materials and Methods --

Animal Collection and Maintenance -- Dungeness crabs, Cancer magister, were trapped in Sequim Bay and the Strait of Juan de Fuca, Washington, and held outdoors in eight 1200-L tanks. Molting and mating crabs were isolated from those to be tested. Seawater, drawn from the entrance to Sequim Bay, entered each holding tank through a manifold under a 15-cm layer of gravel and sand. The crabs readily buried themselves in the sand. Large diameter PVC pipe provided additional shelter. The temperature and salinity of the seawater were 10.4 (± 0.8 S.D.)°C and 30.0 (± 0.1)°/$_{oo}$, respectively; the dissolved oxygen, 6.5 (± 1.6) mg/L and pH, 8.04 (± 0.12). Clumps of blue mussels, Mytilus edulis (L.), provided an ad libitum diet.

Observations of Feeding Behavior In the Field -- Underwater observations using SCUBA diving were made in Possession Sound, Everett, Washington. The site had a shallow, sandy shelf extending from shore and breaking at a depth of 4 m into a steep slope that continued to depths of over 140 m. Observations with SCUBA were confined to depths above 20 m and were concentrated on the shelf and upper portion of the slope. Here were eelgrass beds up to 500 m^2 in area and to the south the sand graded into pebbly sand, pebbles, and then cobbles. Starting from a landmark we repeatedly followed a transect west across the shelf, then at the upper portion of the slope we went either north or south against the prevailing current. A return transect was made over the shelf about 3 to 6 m from the beginning of the slope and paralleling the previous transect. The number of crabs

encountered, their activity, and other behavioral data were recorded *in situ* on waterproof paper. A stopwatch in an underwater case was used to measure the time (sec) for 10 flicks of one antennule in buried crabs. Twelve dives averaging 44 min each were made during daylight at different points in the tidal and seasonal cycles.

Observations of Feeding Behavior In the Laboratory -- Feeding behavior was observed in the outdoor holding tanks described above and in 265-L fiberglass aquaria with glass fronts and sandy substrates. Reactions of individual crabs to clam juice and chopped clam were observed from behind a blind positioned before the glass front.

Determination of Chemosensory Thresholds -- In the apparatus (Fig. 3) modified from Pearson and Olla (1977) crabs were presented with experimental solutions and their subsequent behavior observed. From the main seawater supply, seawater at 10°C passed through wound cellulose filters and a polypropylene filter bag of 100 μm pore size into head tanks that in turn delivered the seawater to four PVC manifolds (6.35 cm diam) each with 10 glass dripper arms. The dripper arms were adjusted to deliver 1.0 L/min into each 5.68-L testing chamber. Seawater passed through a glass funnel into an inlet manifold of plexiglass tubing (12 mm diam) that was connected to the white translucent plexiglass cover clamped to each chamber. Seawater entered each chamber through three slits in the inlet manifold; the bottom one (1 x 26 mm) was horizontal, and the upper two (1 x 30 mm) were at 30° to the horizontal. The three slits were positioned 2, 3, and 4.5 cm from the chamber bottom.

The glass testing chambers were arranged in a single line on four trays; 10 chambers to a tray. Fluorescent lights with a daylight spectrum provided 508 (± 80 S.D.) lux of illumination with a photoperiod synchronized to civil sunrise and sunset. Illumination at night was 0.40 (± 0.18 S.D.) lux. Blinds surrounded the trays so that the crabs could be observed and the experimental solutions added from either side.

The experimental solutions were introduced into each testing chamber *via* the glass funnel receiving the seawater from the dripper arms. A teflon delivery tube (7 mm diam) carried the solution to the funnel from a buret calibrated to deliver 20 mL in 15 sec. Initially, the delivery tubes were inserted through PVC tubes fixed in position, but later this stationary PVC tubing was removed.

To obtain a dilution factor for estimating the effective concentration within a chamber, seawater solutions of azorubin red were introduced, and water samples from six positions within the chamber compared with standard dilutions of the dye solution in a spectrophotometer at 520 nm. During the dye studies the chamber contained a crab model displacing 530 mL, a volume typical of the crabs tested. The peak concentration was in the lower midpoint of the chamber 10 sec after the dye solution was added and was 0.011 (± 0.003) times the concentration of the introduced solution. Therefore, the effective concentration of experimental solutions reported here were calculated by multiplying the concentrations of the introduced solutions by 0.011.

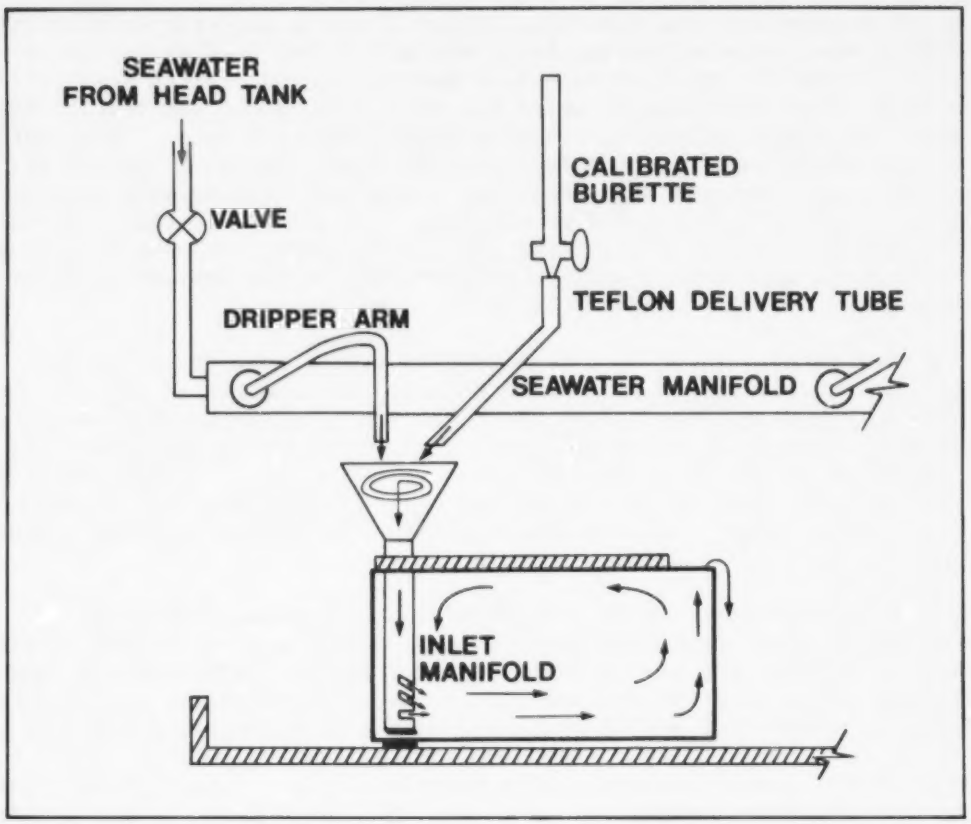

Figure 3. A schematic diagram of the chemosensory testing apparatus. From Pearson et al., 1979.

Because clams have been found to be a major portion of the diet of Dungeness crabs (Butler, 1954; Gotshall, 1977), seawater solutions of a freeze-dried extract of the littleneck clam, Protothaca staminea (Conrad), were presented to the crabs. Clams were held in the laboratory for several days to purge themselves of sediment. The shucked meats and clam liquor were then freeze-dried and stored at -60°C. The resultant freeze-dried clam extract (FDCE) was first powdered in a blender with a stainless steel cup chilled to -60°C, and then stored at -60°C. FDCE stock solutions were prepared by mixing a weighed portion of the powdered FDCE with seawater filtered through a 0.4 µm membrane. After 2 h on a magnetic stirrer, stock solutions were filtered through tared Whatman #4 and GF/C filter paper. FDCE concentrations reported here have been corrected for the loss of the FDCE retained on the filters, which was 48.6 (± 1.5)% of the initial FDCE weight. The stock solutions, which averaged 2.05 (± 0.06)g FDCE/L, were refrigerated and used for no more than five days. Serial dilutions of the stock FDCE solution were made less than 1 h before testing with seawater freshly filtered through a 0.4 µm membrane. An aliquot of the filtered seawater used for dilution constituted the control solution. The experimental and control solutions were kept in a water bath at the ambient seawater temperature and shaken immediately before use.

Approximately 24 h before testing, crabs were transferred to the testing chambers from the holding tanks where they had an ad libitum diet. In preliminary experiments tidal phase was found to influence chemosensory responses. Therefore, while all testing was done during daylight hours, it was synchronized to begin and end within either a rising or falling tide. The seawater for the FDCE dilutions and control was drawn and filtered 1 h after a tidal change. Testing then began as soon as possible and stopped before the next tidal change.

Each day a maximum of 40 crabs were each presented with 20 mL of either one of eight dilutions of FDCE stock solution or a control of filtered seawater. Molting and mating crabs were not tested. The order in which individual crabs were watched and the choice of experimental solution were randomized except that active crabs and ones with retracted antennules were passed over. The identity of the experimental solution was not known to the observer. Individual crabs were observed for 1.0 min prior to introduction of the experimental solution, and their antennular flicking rate and other behavior recorded. The flicking rate of one antennule was measured using a counter activated by a hand-held switch. The experimental solution was then introduced and the observations continued for 1.0 min after the beginning of solution addition. The behavior was scored with criteria selected after observations of feeding in laboratory and field and numerous trials in the apparatus.

A crab was considered to have detected an experimental solution when there was an abrupt change in the orientation of the antennules within 30 sec after solution introduction and if the ratio of the antennular flicking rate for 1.0 min after solution introduction to that for 1.0 min before was 1.50 or higher. The antennular flicking rate for a resting Dungeness crab in the apparatus ranged from 5 to 47 flicks/min with a median of 30 flicks/min (n = 30). In contrast, the flicking rate observed in the field was higher. At 9-11°C observations with SCUBA showed the antennular flicking rate of buried crabs to range from 36 to 103 flicks/min with a median of 70 flicks/min

(n = 27). When crabs were observed for two consecutive minutes in the chemosensory testing apparatus, without any addition of experimental or control solution, the ratio of the antennular flicking rate of the second minute to that of the first ranged from 0.49 to 2.00 and had a median of 0.94 (n = 30). The criterion value of 1.50 was determined a priori from observations of crabs in the testing apparatus following the experimental protocol except no solution was added. After ranking the resultant ratios by magnitude, the ratio at the 95 percentile (n = 30) proved to be 1.50. Thus, the a priori probability that an antennular flicking ratio greater than 1.50 represents a spontaneous increase rather than a reaction to the FDCE was less than 5%.

Feeding behavior was taken to begin when a Dungeness crab probed the substrate with its chelae and/or exhibited a rapid and coordinated movement in which the dactyls and chelae moved to bring an object, under the crab, forward and up to its mouth. These coordinated movements were essentially the same as those described as capture responses by Fuzessery and Childress (1975) for the crab Cancer antennarius. Because the sequence and character of behavior of the Dungeness crab in the testing chambers correspond to that in the laboratory aquaria, the behavioral criteria should be viewed as indicating the onset of feeding behavior that would have led to ingestion, given the presence of food.

At each FDCE concentration the percentage of crabs meeting the assay criteria was recorded. Then the threshold concentration for detection was calculated following the regression analysis of Pearson and Olla (1977). The threshold concentration was that concentration at which 50% of the crabs exhibited the behavior of interest.

Results --

Observations of Feeding Behavior In the Field -- SCUBA observations of Dungeness crabs showed that their activities differed with habitat and tidal phase. During high tides crabs were walking and feeding on the sandy shelf. At low tides crabs were buried on the upper portion of the slope and the number on the shelf, even in the eelgrass, was low. In 6 out of the 12 dives made, feeding behavior was observed. Three Dungeness crabs were seen with clams. The first crab was ingesting the foot, gills, and viscera of a clam. The second was carrying a littleneck clam, Protothaca staminea, held tightly against its body by both chelae. The third crab was carrying and feeding on a butter clam, Saxidomus giganteus (Deshayes). Both valves of the butter clam had been broken away near the siphon, and the crab was inserting one chela and tearing away tissue for ingestion. Four Dungeness crabs were observed feeding on barnacles by using both chelae to hold barnacle covered rocks (1 to 4 cm in diameter) up to the maxillipeds and mandibles, which were crushing the barnacles for ingestion. Red rock crabs, Cancer productus (Randall), were also observed carrying Protothaca staminea and feeding on barnacles.

Observations of Feeding Behavior In the Laboratory -- In aquaria, resting crabs typically had their ventrum touching the sand substrate and chelae drawn up close to or touching the body. The eyestalks were extended but occasionally bobbed into and out of their sockets for a few seconds. The two antennules were often flicking in different directions and at

different rates. When clam juice or a piece of clam was introduced into an aquarium, crabs exhibited an abrupt change in the orientation of the antennules, closely followed by a sharp increase in the antennular flicking rate. The antennules became parallel as they oriented in the same direction, usually upstream. The rate of antennular flicking rose from a base of 20-40 flicks/min to a peak of as much as 120 flicks/min. Rhythmic beating of the maxillipedal flagellae, which is presumptive of gill bailing (Burrows & Willows, 1969), began with, or immediately followed, the changes in antennular behavior. Crabs then rose from the resting position and began walking with the chelae extended forward and held above the substrate surface. The ambulatory dactyls probed the sand with an inward motion. The chelae probed the substrate with inwardly directed, arcing motions across or slightly beneath the sand surface. When a dactyl contacted a clam piece, the clam was quickly swept inward and then forward by the dactyls and upward to the maxillipeds by the chelae, which were simultaneously brought inward and upward. The chelae held the clam while the maxillipeds and mandibles tore off pieces for ingestion. When feeding on live blue mussels, crabs probed the mussel clump with the chelae and then either pulled one mussel away or crushed it in place. Separated or attached mussels were crushed between the fingers of the chelae, which then held pieces of broken mussel shell while the maxillipeds and mandibles cleaned off the adhering tissue. In contrast, the blue crab has been observed by Pearson and Olla (1977) to separate one mussel completely from the clump by cutting the byssum threads and then to pry the valves apart with both chelae as one would open a book.

Determination of Chemosensory Thresholds -- In the chemosensory testing apparatus, specific components of feeding behavior occurred more frequently and intensely with increasing FDCE concentration (Table 9). Thus, when low FDCE concentrations (10^{-16} to 10^{-8} g/L) were introduced, crabs typically showed little or no activity beyond the changes in antennular movement indicative of detection. At high levels (10^{-6} to 10^{-3} g FDCE/L) crabs made probing motions with the dactyls and chelae, especially while walking. The dactyl and chelae probing was sometimes accompanied by movement of the chelae to the mouth. At the highest level (10^{-3} g FDCE/L) crabs rapidly moved the dactyls inward and forward and the chelae inward and upward in the same manner in which, in the laboratory aquaria, they had seized and brought to the maxillipeds clam pieces encountered by the dactyls. Also occurring at the highest extract level was the approach to and manipulation of the inlet manifold, the source of the FDCE-laden seawater.

The detection of the clam extract was distinct and readily discernible. When a crab changed antennular orientation and increased antennular flicking, the flicking ratios were usually considerably above the criterion value of 1.50 (overall median ratio = 2.67, Table 10). Further, the magnitude of the detection response itself did not increase with FDCE level. Although the flicking ratios for all crabs observed differed with FDCE concentration ($P = 0.999$, median test, Conover, 1971), the median ratios for responding individuals did not ($P = 0.379$, median test). Even though the overall median flicking ratio for crabs showing feeding activity (4.61) was higher than that for crabs detecting but not feeding (2.57), the difference was not quite significant ($P = 0.938$, median test). The number of animals detecting, not the magnitude of the detection response, increased with FDCE level, and the percentage of crabs detecting the FDCE was used to determine the threshold concentration.

Crabs readily detected solutions of the clam extract. The percentage of crabs detecting the FDCE was nearly 100% at the highest levels tested and decreased with the FDCE concentration (Fig. 4). The threshold concentration at which 50% of the crabs detected the FDCE was calculated to be 4.8×10^{-10} g/L (Fig. 4). Back calculation of the 95% confidence limits about the Y estimate of 50% showed that the detection threshold could have been as low as 10^{-14} g/L. The percentage of crabs (n = 30) that detected the control seawater was 33.3%.

Because feeding responses only occurred above 10^{-6} g FDCE/L (Fig. 4), there were not enough data for an adequate regression equation. Therefore, a median line was drawn in Fig. 4, and the threshold concentration at which 50% of the crabs began feeding behavior estimated graphically. The feeding threshold was 10^{-2} g FDCE/L, some 8 orders of magnitude higher than the detection threshold.

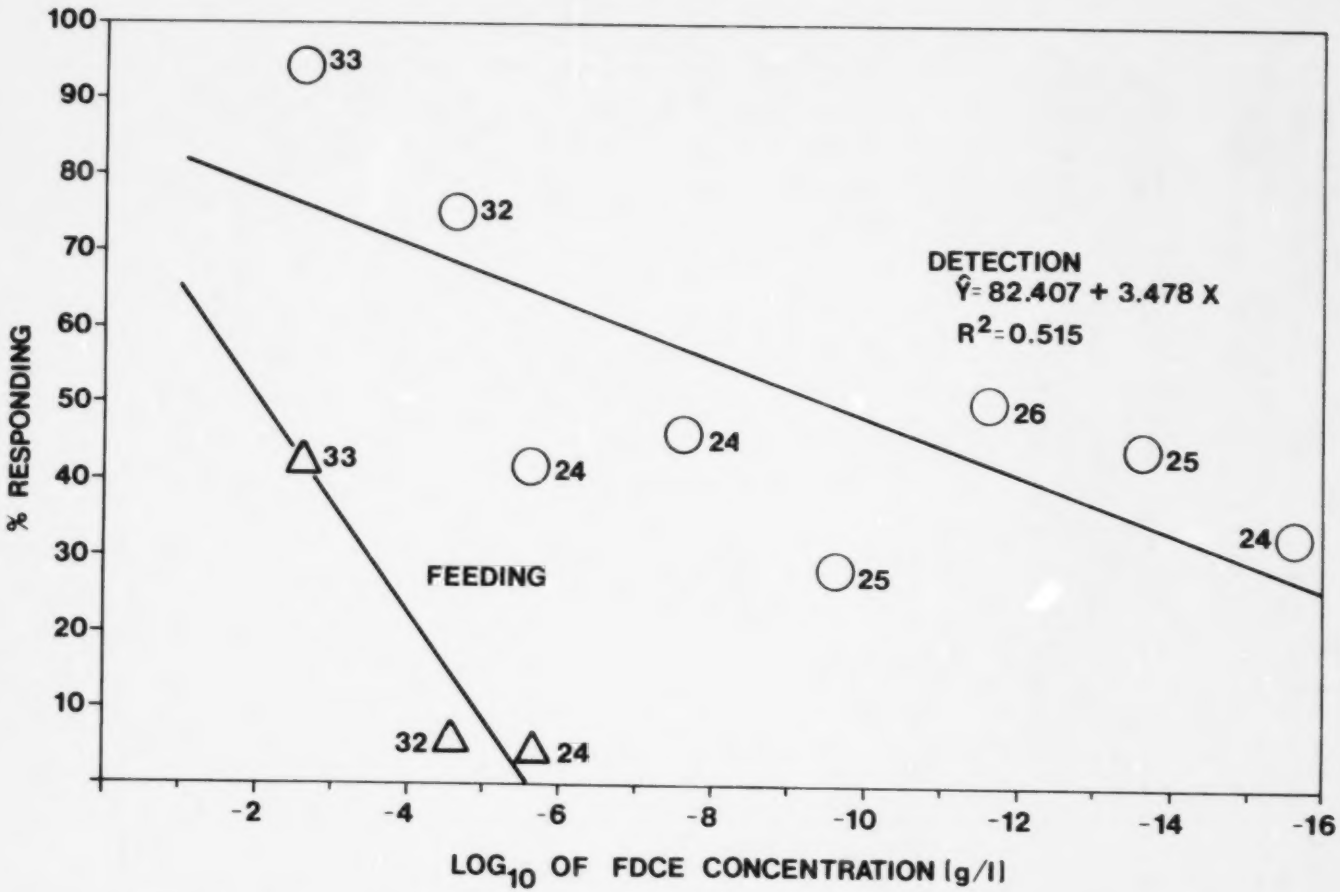

Figure 4. The percentage of Dungeness crabs detecting the freeze-dried clam extract (FDCE) (circles) or beginning feeding behavior (triangles) as a function of the logarithm of the FDCE concentration (g/L) within the testing chamber. The number of crabs at each concentration is indicated. The control seawater was detected by 33.3% of the crabs (n = 30).

From Pearson et al., 1979.

Table 9. The occurrences of specific components of feeding behavior at various FDCE concentrations. The tabulated values are percentages of the total number of crabs observed at each concentration. The control values were not included in the Cox and Stuart tests for trend (Conover, 1971).

BEHAVIOR	Log $_{10}$ of FDCE Concentration (g/L)								CONTROL	Test for Trend P
	-2.6	-4.6	-5.6	-7.6	-9.6	-11.6	-13.6	-15.6		
Change in antennular orientation & increased flicking	93.9	75.0	41.7	45.8	28.0	50.0	44.0	33.3	33.3	.9375
Beating of maxilli-pedal flagellae	90.9	69.8	45.8	33.3	40.0	57.7	36.0	37.5	20.0	.9375
Gaping and labiating of maxillipeds	36.4	6.2	4.2	0	4.0	4.0	4.0	4.0	0	.9375
Antennal whipping	42.4	12.5	16.7	4.2	24.0	7.7	12.0	4.2	6.7	.875
Grooming	9.1	6.2	4.2	8.4	0	7.7	12.0	0	3.3	.6875
Body raising	36.4	12.5	16.7	4.2	8.0	11.5	11.5	4.2	10.0	1.000
Walking	24.2	0	0	0	0	0	0	0	0	---
Dactyl searching	27.3	3.1	16.7	0	4.0	0	4.0	4.2	0	.9375
Chelae probing	42.4	6.2	4.2	0	0	0	0	0	0	1.000
Total No. of Crabs	33	32	24	24	25	26	25	24	30	

From Pearson et al., 1979.

Table 10. The antennular flicking rate ratios at various FDCE concentrations. The ratios were calculated by dividing the flicking rate for 1.0 min after FDCE introduction by that 1.0 min before.

	All Crabs			Crabs fulfilling detection criteria		Crabs detecting but not feeding		Crabs feeding	
Log_{10}[FDCE]	N	Range of Ratios	Median Ratio	N	Median Ratio	N	Median Ratio	N	Median Ratio
-2.6	33	0.88 - 30.7	3.50	31	3.82	17	2.81	14	4.53
-4.6	32	0.26 - 13.8	2.43	24	2.68	22	2.54	2	9.30
-5.6	24	0.50 - 13.0	1.74	10	2.32	9	2.04	1	2.64
-7.6	24	0.68 - 38.0	1.76	11	2.40	11	2.40	0	----
-9.6	25	0.50 - 7.60	1.44	7	2.85	7	2.85	0	----
-11.6	26	0.55 - 5.40	2.35	13	3.17	13	3.17	0	----
-13.6	25	0.33 - 18.0	1.70	11	2.20	11	2.20	0	----
-15.6	24	0.64 - 12.5	1.43	8	3.19	8	3.19	0	----
Control	30	0.01 - 9.60	1.39	10	2.60	10	2.60	0	----
Total	243	0.01 - 38.0	1.78	125	2.67	108	2.57	17	4.61

From Pearson et al., 1979.

Discussion --

The antennules of many decapods have been shown to function as distance chemoreceptors (Hazlett, 1971a), and now for at least three decapods changes in antennular behavior have been found to indicate chemical detection. For the blue crab, Callinectes sapidus, abrupt increases in the antennular flicking rate accompanied by the onset of vigorous and continuous rhythmic beating of the maxillipedal flagellae indicated detection not only of a clam extract but also of the petroleum hydrocarbon naphthalene (Pearson & Olla, 1977, 1979). The antennular flicking rate increased upon presentation of glycine or glutamic acid to the spiny lobster, Panulirus argus, (Price & Ache, 1977). With the Dungeness crab an increase in flicking rate along with a change in orientation also indicated detection of a clam extract. In addition, Mackie and Shelton (1972) and Fuzessery and Childress (1975) reported increased antennular flicking in several crustaceans as the first indication of "awareness" of sapid solutions but did not incorporate antennular flicking into their measurements of chemosensory ability.

Antennular flicking is widespread among crustaceans, and several explanations for the function of flicking in chemoreception have been given. Snow (1973) suggested that flicking in a hermit crab facilitated chemoreception by splaying out the aesthetasc hairs and thereby increasing the passage of water over the chemoreceptors. The neurophysiological observation that flicking produced renewed nervous response after fading of the initial response led Price and Ache (1977) to propose that an increased rate of flicking served to extend the time period during which the chemoreceptors of the lobster were sensitive. After suggesting that antennular flicking in the lobster was analogous to sniffing in vertebrates, Fuzessery (1978) discussed how flicking may be involved in orientation to odor. Our observations that antennular flicking increases in the presence of sapid chemicals in Callinectes sapidus and Cancer magister are more presumptive evidence that flicking enhances chemoreception in some way but do not allow us to choose any one explanation from among those proposed.

Interspecific comparisons of chemosensory ability are difficult because experimental techniques and, especially, criteria vary greatly, and of the other crustaceans studied only three appear comparable on the basis of close phylogeny or similar experimental treatment. The best comparison is between blue and Dungeness crabs because the behavioral criteria and the testing methods were essentially the same. The detection threshold for the blue crab was 10^{-15} g/L (Pearson & Olla, 1977), which is 5 orders of magnitude lower than that found here for the Dungeness crab (10^{-10} g/L). The lobster, Panulirus argus, presented with the amino acids glycine and glutamic acid, showed increased antennular flicking at 10^{-10} M (about 10^{-8} g/L), the lowest concentration tested (Price & Ache, 1977). Our regression of the data of Fuzessery and Childress (1975) showed the threshold concentration for the release of feeding motions by an equimolar mixture of three amino acids to be 10^{-9} g/L for the crab Cancer antennarius. Amino acids alone and in combination have been found to be less attractive than food extracts (Shelton & Mackie, 1971; Mackie, 1973) so that we would predict that testing with a food extract would yield lower thresholds in P. argus and C. antennarius.

The feeding threshold for the Dungeness crab was not distinct from that found for the blue crab. The feeding thresholds for the blue crab

varied from 10^{-1} to 10^{-3} g FDCE/L (Pearson & Olla, 1977). In comparison the Dungeness crab had a feeding threshold of 10^{-2} g FDCE/L. For both crabs the feeding thresholds were many orders of magnitude above those of detection.

There are several explanations for the difference in the detection thresholds seen for Callinectes sapidus and Cancer magister. Ultimately the threshold differences derive from ecological and evolutionary differences. Proximately the threshold differences may derive from differences in the morphology and movement of the antennules. Although a larger crab than the blue crab, the Dungeness crab has smaller antennules. When flicked through equal arcs the smaller antennules of Cancer magister would sweep out a smaller water volume than those of Callinectes sapidus. In addition, the flicking rate of a resting Dungeness crab (30 flicks/min) is less than that of a resting blue crab (85 flicks/min). Given equal numbers of chemoreceptors per unit surface area, a resting Dungeness crab could be sampling a smaller volume of water per unit of time than a similar blue crab and, consequently, would exhibit a higher threshold. Perhaps detailed morphometric analysis could relate increasingly chemoreceptive area to decreasing thresholds in a series of crustaceans.

Blue and Dungeness crabs live under two different natural regimes of temperature. The two species were tested at temperatures 10°C apart, and this temperature difference may partially account for the difference in detection thresholds. At 10°C Dungeness crabs feed, mate, and are generally active while at the same temperature blue crabs feed little, if at all, (Leffler, 1972) and are lethargic and intermittently dormant (Olla & Pearson, unpubl.). It is, therefore, doubtful that testing both species at the same temperature would produce a meaningful comparison.

Field observations reported here and elsewhere (Butler, 1954; Gotshall, 1977) have shown that Dungness crabs find, capture, and consume clams and small crustaceans buried in the sand. In our laboratory and in the field (Butler, 1954) crabs search for buried prey by probing the substrate with their dactyls and chelae. During such searching the crab uses both chemical and tactile cues, and Fuzessery and Childress (1975) suggest that because the capture responses seen both here and in their study occur with chemical cues alone, chemoreception predominantly controls the location and capture of prey.

Before searching intensely with dactyls and chelae, however, the crab has found, presumably through some chemical cue, a site potentially productive of food, and it is in finding such a site that the efficiency with which the antennules function in distance chemoreception influences foraging success. Generally as the chemosensory thresholds lowers, the active space widens (Wilson, 1970). With the two threshold values given here and field measurements of current velocities one could construct two active spaces. The first would predict the area within which a crab can detect the presence of an aggregation of clams, and the second, the area within which the crab begins active search for buried prey. This type of analysis has obvious application to ecological questions, especially those concerning predator-prey relationships.

B. Impairment of Chemosensory Food Detection in the Dungeness Crab, Cancer magister, by Petroleum Hydrocarbons

For marine organisms, disruption of chemoreception by oil is viewed as both likely and of important ecological consequence (Blumer, 1969; Olla & Samet, 1974; Olla et al., 1980a). Chemosensory disruption by various petroleum hydrocarbons and oil fractions has been reported in snails (Jacobsen & Boylan, 1973; Hyland & Miller, 1979), lobsters (Atema & Stein, 1974), and in shore crabs (Takahashi & Kittredge, 1973). In some of these early studies the exposure regime was not well defined and did not always compare well with the length and level of exposure likely to be encountered in an actual oil spill. Here we report on the ability of the Dungness crab, Cancer magister, to detect and respond to a food extract after 24-h exposure to seawater contaminated with Prudhoe Bay crude oil. To improve the correspondence of our petroleum exposure to that of actual situations, we exposed and tested crabs in a continuously-flowing seawater system at an oil level reasonably expected to occur during an oil spill.

Behavioral criteria can be used to measure the acuity of chemoreception in various organisms (Olla et al., 1980a). Changes in antennular behavior indicate that detection of a clam extract occurs at 10^{-15}g/L for the blue crab, Callinectus sapidus, (Pearson & Olla, 1977) and at 10^{-10}g/L for the Dungeness crab (Pearson et al., 1979). Such high sensitivity implies high dependence on chemoreception in finding food.

To determine whether exposure to petroleum hydrocarbons impaired this acute detection ability, we exposed Dungeness crabs to oil-contaminated seawater for 24 h, presented them with a clam extract in the presence of the oil-contaminated seawater, and recorded the percentages of crabs showing the changes in antennular behavior indicative of detection and of those showing the chelae probing indicative of food searching. At 24 h and 48 h after stopping the flow of oil-contaminated seawater, we retested the crabs to determine the time period necessary for recovery of detection ability. Because this first experiment indicated rapid recovery, we performed a similar second experiment in which we presented the clam extract to crabs 1 h after stopping the flow of contaminated seawater.

Materials and Methods --

Animal Collection and Maintenance -- Dungeness crabs, Cancer magister (Dana), trapped in the Strait of Juan de Fuca, Washington, were held under the conditions described by Pearson et al. (1979). Seawater temperatures during the two experiments were 8.9 (± 2.7 S.D.)°C (n = 16) and 9.2 (±0.5)°C (n = 16); salinities, 31.8 (±0.4)°/$_{oo}$ (n = 5) and 32.0 (±0.0)°/$_{oo}$ (n = 4); and dissolved oxygen 7.6 (±0.7) mg/l (n = 16) and 8.0 (±0.3) mg/l (n = 9). Clumps of blue mussels, Mytilus edulis, and live clams, Protothaca staminea, provided an ad libitum diet.

Experimental Apparatus -- We coupled the oil delivery system developed by Vanderhorst et al. (1977), and used extensively by Anderson et al. (1979, 1980a & b), to the chemosensory testing apparatus of Pearson et al. (1979). Oil-contaminated seawater was delivered to 20 of the 40 chemosensory testing chambers from dripper arms situated along manifolds connected to the oil delivery system. Contaminated water entered each exposure

chamber at 0.1 L/min while clean water entered at 0.9 L/min. Control chambers received clean water at 1.0 L/min. Seawater entered each chamber through a glass funnel connected to a slotted inlet tube within the chamber. Teflon tubes carried seawater solutions of the clam extract to the funnels from burets calibrated to deliver 20 mL within 15 sec. Previous dye studies of Pearson et al. (1979) showed that the maximum concentration of an introduced solution within a chamber occurs 10 sec after introduction and is 0.011 (±0.003) times the concentration of the introduced solution.

The delivery system produced oil-contaminated seawater that was largely a water-soluble fraction with some finely dispersed droplets. The chemical composition of this oil-contaminated seawater has been well characterized by Bean et al. (1978) and reported in detail by Anderson et al. (1979; 1980a). Here we sampled seawater in the testing chambers by the resin column absorption technique of Bean et al. (1978) and analyzed the samples by infrared (IR) spectrophotometry. The data of Bean et al. (1978) and Anderson et al. (1979, 1980a) show the correlations between the values determined by IR and the concentration of specific hydrocarbons determined by other methods for the same system. To determine how fast hydrocarbon concentrations dropped after stopping the flow of oil-contaminated water in the second experiment, we supplemented IR analyses with analyses for mono-aromatic hydrocarbons by a helium gas partitioning technique modified from McAuliffe (1971).

Experimental Solutions -- The experimental solutions were seawater solutions of freeze-dried clam extract (FDCE) of littleneck clam, Protothaca staminea. The solutions were prepared following Pearson et al. (1979). Stock solutions averaging 1.89 (±0.12) g FDCE/L (n = 6) for the first experiment and 2.06 (±0.22) g FDCE/L (n = 5) for the second were refrigerated and used within five days. A 10^{-6} dilution of the stock FDCE solution was made 1 h before testing with seawater freshly filtered through a 0.4 µm membrane. An aliquot of the filtered seawater used for dilution was used as the control solution. All solutions were held in a water bath at ambient seawater temperature.

Procedures -- After the oil delivery system had been operating for several days and the hydrocarbon concentrations examined, a single Dungeness crab was added to each of the 20 exposure and 20 control chambers. Chemosensory testing was synchronized to begin and end within either a rising or falling tide and after 24 h exposure to oil-contaminated seawater. In the first experiment, the FDCE solutions were presented with oil-contaminated seawater still flowing through the chambers. Each crab was presented with either one of two dilutions of FDCE or a control of filtered seawater. After correction for dilution within a chamber, these FDCE concentrations were 10^{-2} and 10^{-8} g/L. The choice of dilution and the order of presentation were randomized except that active crabs and those with retracted antennules were passed over. The observer did not know the identity of any solution. An individual crab was observed for 60 sec prior to introduction of experimental solution, and the antennular flicking rate and other behavior recorded. The observer depressed a switch of an event counter for each flick of one antennule. The solution (20 mL) was then introduced and observation continued for another 60 sec from onset of introduction.

The criteria of Pearson et al. (1979) were used to score the behavior. Detection was indicated when a crab abruptly changed antennular orientation and increased antennular flicking rate so that the ratio of the rate after solution introduction to that before was 1.50 or higher. Previous observations indicate that the a priori probability that such an increase in antennular flicking is spontaneous, rather than in response to the solution, is less than 5% (Pearson et al., 1979). The onset of food searching was indicated when a crab probed the substrate with its chelae or exhibited the capture response described by Pearson et al. (1979).

To examine recovery of detection ability, we stopped the flow of oil-contaminated water after the first presentation of FDCE. Clean seawater then entered the chambers at 0.9 L/min. After 24 h and 48 h both exposed and control crabs were again presented with experimental solutions and their behavior observed and scored.

Because the first experiment indicated rapid recovery, we wished to see if such recovery could occur within one hour and, therefore, repeated the exposure phase of the first experiment. Instead of presenting FDCE with oil-contaminated water still present, we turned off the contaminated water and presented the FDCE 1 h later. The start and finish of exposure for individual crabs was staggered to achieve this one-hour clearance of oil from the chambers.

Statistical Analysis -- The experiments were run until about 30 crabs had been tested under each experimental condition. The numbers of crabs detecting and not detecting the various experimental solutions were totaled for exposed and control conditions. Although data is presented as the percentage of crabs detecting the FDCE, chi-square analysis was done on 2 x 2 contingency tables of the number of crabs detecting or not detecting under control or exposed conditions. Data for crabs showing chelae probing was treated similarly.

Results --

Hydrocarbon Concentrations -- During the first experiment, where the clam extract was presented in the presence of oil-contaminated seawater, the total hydrocarbon concentrations by IR analyses were 0.27 (±0.04) ppm (n = 22) during the 24-h exposure and 0.013 (±0.004) ppm (n = 6) 24 h after the oil-contaminated water was stopped. During the second experiment, where the clam extract was presented 1 h after stopping the oil-contaminated seawater, the total hydrocarbon concentration by IR averaged 0.34 (±0.07) ppm (n = 10). Also, in the second experiment after 1 h the concentration of monoaromatic hydrocarbons (Table 11) fell to 0.008 times the exposure level.

Impairment and Recovery of Chemosensory Detection -- After 24-h exposure to and still in the presence of oil-contaminated seawater, the percentages of exposed crabs detecting the clam extract was about half those of control crabs (Table 12). In contrast, the percentage of crabs probing with chelae did not differ significantly between control and exposed conditions (Table 13). Some exposed individuals presented with 10^{-2} g FDCE/L probed the substrate with their chelae without the normally proceeding changes in antennular behavior.

Recovery of detection ability occurred rapidly. In the first experiment the percentage of crabs detecting FDCE at both levels did not differ between control and exposed conditions for both 24 h and 48 h (Table 12). In the second experiment, where the FDCE was presented 1 h after the flow of oil-contaminated seawater was stopped, again the percentage of crabs detecting did not differ significantly between control and exposed conditions (Table 14).

Table 11. The concentrations of monoaromatic hydrocarbons in the chemosensory testing chambers. Determined by helium gas partitioning, n = 4.

	HYDROCARBON CONCENTRATIONS (PPB)	
Hydrocrabon	During 24 h of Continuous Flow $\bar{x}$ ± S.D.	1 h after flow Stopped $\bar{x}$ ± S.D.
Benzene	50.1 ± 10.8	0.13 ± 0.24
Toluene	85.0 ± 12.7	0.16 ± 0.31
Ethyl Benzene	13.8 ± 2.8	0.74 ± 0.95
m + p Xylene	38.0 ± 5.2	0.94 ± 1.36
o Xylene	19.5 ± 3.4	0.90 ± 1.22
Total Trimethyl Benzenes	40.6 ± 11.9	<0.01
TOTAL	247.0 ± 34.7	1.98 ± 3.76

Table 12. Percentage of Dungeness crabs detecting the clam extract [FDCE] after exposure to continuously-flowing sea water contaminated with Prudnoe Bay crude oil.

[FDCE] g/L	Treatment	AFTER 24-H EXPOSURE No. of Crabs Tested	% Detecting	x^2	p	AFTER 24-H IN CLEAN WATER No. of Crabs Tested	% Detecting	x^2	p	AFTER 48-H IN CLEAN WATER No. of Crabs Tested	% Detecting	x^2	p
10^{-2}	Control	32	97	16.0	0.999	37	95	1.18	0.723	31	97	1.96	0.838
	Exposed	30	53			31	87			31	87		
10^{-8}													
	Control	34	32	3.46	0.937	38	42	0.05	0.177	31	36	1.06	0.697
	Exposed	31	13			33	39			31	48		
Control													
	Control	18	17	0.40	0.473	17	35	0.13	0.282	16	40	1.97	0.840
	Exposed	20	25			22	41			17	18		

Table 13. Percentage of Dungeness crabs probing with the chelae upon presentation of a clam extract [FDCE] after exposure to continuously-flowing sea water contaminated with Prudhoe Bay crude oil.

[FDCE] g/L	Treatment	AFTER 24-H EXPOSURE No. of crabs Tested	% Detecting	x^2	p	AFTER 24-H IN CLEAN WATER No. of crabs Tested	% Detecting	x^2	p	AFTER 48-H IN CLEAN WATER No. of crabs Tested	% Detecting	x^2	p
10^{-2}													
	Control	32	97	2.18	0.860	37	84	0.114	0.265	31	84	2.20	0.862
	Exposed	30	87			31	81			31	68		
10^{-6}													
	Control	34	6	0.329	0.434	38	5	0.395	0.470	31	0	1.02	0.687
	Exposed	31	10			33	9			31	3		
Control													
	Control	18	0	0.924	0.664	17	0	0.793	0.627	16	6	1.10	0.765
	Exposed	20	5			22	4			17	0		

Table 14. Percentage of Dungeness crabs responding to a clam extract [FDCE] presented in clean water 1 h after a 24-h exposure to oil-contaminated sea water.

[FDCE] g/L	Treatment	No. of Crabs Tested	CRABS DETECTING %	x^2	p	CRABS CHELAE PROBING %	x^2	p
10^{-2}								
	Control	28	96	0.002	0.040	89	0.952	0.671
	Exposed	30	97			80		
10^{-8}								
	Control	33	42	0.551	0.542	0	1.118	0.710
	Exposed	30	33			3		
Control								
	Control	19	37	0.681	0.591	0		
	Exposed	13	23			0		

Discussion --

The hydrocarbon concentration to which we exposed crabs were typical of those found during actual oil spills. McAuliffe et al. (1975) estimated that concentrations of hydrocarbons dissolved in the water column reached 0.2 ppm during a spill from an oil platform. About one half of these dissolved hydrocarbons were the monoaromatics present in our system at 0.2 ppm (Table 11). During another platform spill hydrocarbon concentrations between 0.1 and 0.4 ppm were found in the water column by Grahl-Nielsen (1978). Because alkanes were detected, these concentrations represent emulsified oil as well as dissolved hydrocarbons. During the AMOCO CADIZ spill initial measurements of the subsurface water of the L'Aber Wrach estuary showed hydrocarbon concentrations between 0.026 to 0.330 ppm (Wolfe, 1978). Measurements with a towed fluorometer showed that oil-in-water concentrations exceeded 0.5 ppm throughout the estuary and rose above 1.0 ppm in shoal areas (Calder & Boehm, in press). These high levels resulted from turbulent mixing of surface mousse into the water column, and here, too, the detection of alkanes indicated an oil-in-water emulsion. Because the contaminated water produced by our oil delivery system contains predominantly dissolved monoaromatics and very little alkanes (Bean et al., 1978; Anderson et al., 1980a), our exposure regime best represents the platform spill characterized by McAuliffe et al. (1975) and our results indicate more the effects of dissolved hydrocarbons than of emulsified oil.

Decapod crustaceans have two chemoreceptor systems, one for distance chemoreception (seated in the antennules) and another for contact chemoreception (seated in the dactyls, chelae, and mouthparts) (Luther, 1930; Case & Gwilliam, 1961; Levandowsky & Hodgson, 1965; Hazlett, 1968; 1971 a & b). The observation that exposed crabs showed chelae probing but no increases in antennular flicking when presented with FDCE suggests that 24-h exposure to oil-contaminated seawater depressed the functioning of the distance chemoreceptor system in Dungeness crabs while, at least as far as we can determine, not significantly affecting the contact chemoreceptor system. Perhaps longer exposure would have affected the contact chemoreceptor system.

The rapid recovery of detection ability suggests that the disruptive effects of oil exposure may be due to masking of the extract odor or anesthesia of the chemoreceptors, rather than direct cellular damage. Cellular damage would have required a recovery period of days while masking or anesthesia would have been readily reversible upon return to clean seawater (Johnson, 1977; Olla et al., 1980a). In addition to causing a readily reversible effect, the oil-contaminated seawater contained several monoaromatic hydrocarbons known to reduce anesthesia or reversible narcosis in barnacle larvae (Crisp et al., 1967). Whereas direct cellular damage is easily eliminated as the mechanism behind the chemosensory impairment, a recovery time of one hour does not eliminate either masking or anesthesia as alternatives. Another mechanism, not so likely in our system but quite possible in an actual oil spill, is disruption of antennular functioning through physical effects on the sensory hairs, e.g. coating of surfaces or matting hairs together.

Practically, the disruption of the distance chemoreceptor system indicates that under oil spill situations the presence of dissolved hydro-

carbons could cause the Dungeness crab some difficulty in finding food. The apparent intactness of the contact chemoreceptor system implies that the crab may have to touch food to detect its presence. Because chemical stimulation of the antennules apparently is necessary to sustain food searching when contact with food is not direct and immediate (Hazlett, 1971a & b), difficulty in food gathering even after contacting food is quite possible under exposure to oil-contaminated seawater.

Because the radius of the active space within which an organism detects a chemical cue is inversely proportional to the chemosensory detection threshold (Bossert & Wilson, 1963), we can roughly calculate how oil exposure decreases the active space for Dungeness crabs. By lowering the FDCE detection threshold about 10^4 times oil exposure decreases the radius of the active space by 10^4 times. To maintain the same rate of prey capture as the presence of petroleum hydrocarbons shrinks the active space, the Dungeness crab may be required to change its foraging behavior to rely on other sensory modalities, perhaps touch. Fortunately, the recovery data suggests that the necessity of such changes may be relatively transient if the duration of exposure is transient.

C. Effects of Oiled Sediment on Predation of the Littleneck Clam, Protothaca staminea, by the Dungeness crab, Cancer magister.

Oiling of the sediment is increasingly viewed as an important determinant of long-term ecological effects of oil pollution (Wolfe et al., 1977; Cabioch et al., 1978). A good example is the 1969 West Falmouth Oil Spill. After four years the benthic fauna was still undergoing rapid changes in densities and species composition (Sanders, 1978). After seven years high concentrations of oil still persisted, (Burns & Teal, 1979) and exposure to oiled sediment was still producing lowered population densities in the fiddler crab, Uca pugnax, through impaired escape behavior and abnormal burrowing (Krebs & Burns, 1977). Because oil disrupts detection of chemical food cues (Jacobsen & Boylan, 1973; Takahashi & Kittredge, 1973; Hyland & Miller, 1979; Pearson et al., in prep.), oiled sediment may produce another more subtle behavioral effect, disruption of chemosensory-directed predation on buried prey. Oiled sediment would, thereby, affect not only the process of predation itself, but also ecosystem structure and function. One predator-prey system perhaps vulnerable to the effect is crab predation, which substantially influences species composition of soft-bottom communities (Virnstein, 1977; Woodin, 1978; Reise, 1979) and may affect bivalve distribution (Williams, 1978). Here we report field and laboratory experiments that examined how oiled sediment influenced predation on the littleneck clam, Protothaca staminea, by the Dungeness crab, Cancer magister.

Clams are a major portion of the diet of Dungeness crabs (Butler, 1954; Gotshall, 1977) and Pearson et al. (1979) observed Dungeness crabs in the field feeding on littleneck clams. Because the Dungeness crab readily detects extracts of the littleneck clam (Pearson et al., 1979) and chemosensory detection of this extract is reduced by exposure to Prudhoe Bay crude oil in a continuous flow system (Pearson et al., in prep.), we hypothesized that crabs would consume less clams buried in oiled sediment because of impaired chemosensory ability. However, in two experiments with field enclosures crabs consumed more clams on oiled than clean sediment. A

subsequent laboratory experiment then indicated that the observed increase in predation was in part due to increased prey accessibility from oil-induced changes in clam burrowing behavior.

Materials and Methods --

Field Experiments -- In two experiments lasting 13 and 29 d, we used field enclosures to determine the rates of crab predation on clams buried in oiled sediment. Cages similar to those of Virnstein (1977) were constructed by bending and welding steel rod normally used for reinforcing concrete (0.95 cm dia) into a frame 100 x 100 x 30 cm high. Polypropylene/polyethylene screening of 3.2 x 5.5 cm mesh covered the cage sides and top. A square frame of reinforcing rod formed a top that could be completely opened. Rods extending from each corner 60 cm into the bottom anchored each cage. Within each cage a wooden box (95 x 95 x 15 cm deep) with a screened bottom was buried flush with the existing bottom and received the experimental sediment and clams.

On the southern side of Travis Spit, Sequim Bay, Washington, eight cages in two equal groups were set parallel to shore at a tidal height of -0.76 m (-2.5 ft). Five meters separated each cage within a group, and eighteen meters separated the two groups. In both experiments four cages randomly received 135 L of clean sand and four cages, oiled sand. In the 29-d experiment an additional cage set between the two groups also received oiled sand and was used to monitor oil concentration during the experiment. During both experiments water depth varied tidally from 0.1 to 3.4 m. Water temperatures were 14.5 (±1.4 S.D.)°C (n = 49) and 14.6 (±1.6)°C (n = 220), for the first and second experiments, respectively. Salinity was 32.0 (±0.1)°/$_{oo}$ (n = 11). Measurements of current velocity with parachute drogues ranged from 2.0 to 16.1 cm/sec with a median of 5.0 cm/sec (n = 72) and indicated current velocity to be a function of wind and tide. Current velocity measured with a direct reading current meter surrounded by the same mesh covering the cages averaged 2.2 (±0.6) cm/sec over four 6-h periods during which the tide rose 3.2 (±0.1) m.

To produce oiled sand with a nominal concentration of 10000 ppm, 135 L of coarse washed sand (Geometric mean size = 1.2 mm) was mixed with 1350 mL of Prudhoe Bay crude oil in a cement mixer for 30 min. Equal amounts of oil and seawater were stirred in a high speed blender for 30 sec before being mixed into the sand. The minimum of additional seawater necessary to yield a smoothly flowing mixture was added to the cement mixer. We expected that during the addition of oiled sand to the cages the oil concentration would fall to between 10 and 20% of the nominal value. Such reduction would have produced an oil concentration typical of polluted sediment (Clark & MacLeod, 1977).

To find the actual oil concentration of sediment in the cages, two types of composite core samples for hydrocarbon analysis were taken from every cage at the beginning and end of both experiments. Because we expected more rapid loss of oil from the surface, we took short (6 cm) and long (15 cm) sediment cores of 2.5 cm diameter. From control and oiled cages three composite samples, each composed of five long cores, were taken. From oiled cages six composite samples of eight short cores were taken. Total oil levels were measured in three long core and three short core composite

samples from each cage by infrared spectrophotometry (Simard et al., 1951; Anderson et al., 1979). Some of the remaining short-core composite samples were analyzed for any changes in the relative proportion of hydrocarbons by glass capillary gas chromatography (Anderson et al., 1978). During the 29-d experiment one composite sample of 6 cm cores was taken every two to three days from the additional cage and analyzed for total oil concentration.

Littleneck clams, Protothaca staminea, collected from Sequim Bay were divided by shell length into four size classes (26-35, 36-45, 46-55, and 56-65 mm). For each size class we used a differently colored permanent ink to mark the umbo region. In the 13-d experiment each cage received 10 clams in each size class; in the 29-d experiment, 12 in each class. These densities, 40 and 48 clams/m^2, were typical for Sequim Bay (Vanderhorst & Wilkinson, 1979). One day after oiled sand had been added to the cages, clams were placed randomly on the sand surface of every cage and allowed to bury. Clams remaining on the surface the following day were buried.

One male Dungeness crab (carapace length 14.1 (±0.3)cm and 15.2 (±0.7) cm for 13-d and 29-d experiments) was placed into each cage two days after addition of the clams. Observations were made by SCUBA or snorkeling every one to two days. Divers recorded the number of clams in each size class that were unburied but intact as well as those eaten. The number of visible siphons of buried clams, and the position and behavior of each crab within a cage and of other animals around the cage were recorded. Every two to four days divers carefully opened each cage and removed and saved all visible shells and shell fragments. If needed, the mesh of the cages was brushed clean. We counted the number of colored shells recovered to estimate the number of clams in each size class consumed by the crabs.

To confirm the consumption of clams estimated by counting recovered shells, we removed the uneaten clams remaining at the end of each experiment. To see whether clams were buried shallower in the oiled sand, sand and clams from all cages were carefully removed layer by layer and the clams found at several depths were sorted by size and counted. In the 13-d experiment, 2.2% (n = 320) of the clams added were not recovered either as shells during the experiment or intact at the end. In the 29-d experiment we could not account for 2.6% (n = 384) of the clams added. Data analysis was based only on the clams recovered. In the 29-d experiment data from one oiled cage where the crab died was not used.

Laboratory Experiment -- To test whether the increased predation rate on clams in oiled sediment observed in both field experiments was due to shallower burial, a 19-d laboratory experiment examined the predation rate on clams buried in two different depths of sand. Eight 1100-liter tanks (2.2 x 1.1 x 0.6 m) constructed of 1.2 cm plywood coated with finishing type fiberglass resin were divided in half lengthwise by opaque fiberglass dividers to yield chambers of the same surface area as the field enclosures. Filtered seawater (13.1 (±1.0)°C, 32.0 (±0.1)°/$_{oo}$, 6.9 (±0.2) mg DO/L) entered each tank at 5 L/min through a 2.5 cm diameter PVC pipe positioned in the middle of one end behind a fiberglass baffle that extended the width of the whole tank. Holes were drilled on a 2.5 cm square grid across the entire baffle and hole sizes adjusted to promote an even cross-sectional flow through the tank. An identical baffle was positioned downstream 5 cm before a solid fiberglass plate. After passing through the downstream baffle, seawater spilled over the 47-cm high end plate into a drain.

Daylight illumination (238 ± 115 lux) was provided by daylight spectrum flourescent lighting on a photoperiod synchronized to civil sunrise and sunset. Night illumination from incandescent bulbs was adjusted to less than one lux to simulate moonlight.

The 16 chambers provided four replicates of the following treatments: shallow-oiled (5 cm depth of oiled sand), shallow-clean (5 cm of clean sand), deep-oiled (10 cm of oiled sand), and deep-clean (10 cm of clean sand). Preparation of oiled sand was identical to that for the field experiments except that all sand for the laboratory experiment was washed over a 0.32 mm mesh screen to remove fine silts. Composite samples of five cores of 1.9 cm diameter were taken from each tank at the end of the experiment, and total oil concentration was determined by the IR analysis used in the field experiments. In other experiments (Pearson et al., in prep.) the total oil concentration after the sand had stood 24-h in the tanks with flowing seawater was 2690 (±957) ppm (n = 42).

Each chamber received 12 marked littleneck clams in each of the four size classes used in the field. One day after the oiled sand had stood in running seawater, the clams were randomly placed on the sand and allowed to bury. Those remaining on the surface the following day were partially buried, siphon end uppermost, and were found completely buried the next day. At this time one Dungeness crab (carapace width 15.5 ± 0.56 cm) was placed into each chamber.

Initially crabs were observed once an hour to determine when feeding activity occurred. Although most feeding occurred at night, some occurred in late afternoon so that detailed observations on feeding behavior were taken from 1600 to civil sunset. Shells from eaten clams were removed at least once each day and the number in each size class recorded. Also, the number of intact unburied clams was recorded at least once a day. At the end of the experiment we measured the shear strength of the sand in the four treatments with a hand-held shear vane and then recovered all remaining uneaten clams. Of the clams added, 2.3% (n = 768) were not recovered as shells or intact clams. Data from one oiled chamber in which the crab died were not used.

To estimate the weight of clams consumed by the crabs, we used length-weight data on littleneck clams collected from Sequim Bay. The shell lengths of 30 clams in each of the four size classes were measured individually, the clams shucked, and all tissue within the shell blotted dry and weighed. From the data the regression equation, $W = 2.089 \times 10^{-5} L^{3.32}$, related the shucked wet weight (W) in g to the shell length (L) in mm. The weight of clam consumed by a crab during an experiment was estimated by summing over all size classes the total number of clams in a size class times the shucked wet weight for the median shell length in that size class determined from the regression equation.

Results --

Oil Concentration in Sand -- The concentration of oil in the surface sand dropped slightly but not significantly in the 13-d field experiment (Table 15). In contrast, the oil concentration dropped to 12% of its initial value in the 29-d field experiment. The difference in initial oil

levels between the two field experiments was derived from a greater water depth and slight current occurring while oiled sand was being added to the cages in the 13-d experiment. Along with the overall decline in total oil concentration in the 29-d experiment, the aromatic hydrocarbons showed a slightly higher decline than the saturates (Table 16). Within these two classes, relative proportions of individual hydrocarbons changed little or not at all. Oil droplets were observed rising from the sand when crabs burrowed or otherwise disturbed the sand so that the rate at which oil was released from the sand was undoubtedly related to the activity of the crabs. Oil concentration within the cage, monitored every two or three days, did not show a steady decline probably because patches of undisturbed sand of high oil concentration persisted amidst disturbed sand of much reduced oil concentration.

In the 19-d laboratory experiment the oil concentration dropped to 1044 (±329) ppm (n = 16) and 1185 (±409) ppm (n = 16) in the shallow-oiled and deep-oiled sand. These concentrations were slightly less than half the initial oil level.

Crab Predation On Clams -- We observed Dungeness crabs unearthing littleneck clams with their chelae and dactyls. Crabs unearthed more than they consumed and opened large (>45 mm) clams differently than small (<45 mm) ones. Small clams were usually crushed, and we recovered not whole valves but small fragments. Large clams were pried open after being held for several minutes. After picking up a large clam, a crab tumbled it until the clam was held against the body with the inside of one chela. The umbo faced the elbow of the cheliped and the commissure between the valves was horizontal. The crab spread the fingers of its other chela and placed their tips into the commissure between the valves. After holding this position for several minutes, many crabs dropped the clam and moved away. Where a crab continued holding a clam, we could not discern whether the crab then forced the valves apart by wedging in its fingertips or simply waited until the clam relaxed slightly and inserted the fingertips in the gap. Once the fingertips were inside, the crab would quickly pry the valves apart. Shells from large clams were usually recovered intact or with chipping or partial breakage along the valve edge.

Effects of Oiled Sediment -- In both field and laboratory experiments crabs ate significantly greater numbers and weights of clams from oiled than clean sand (Table 17). During the field experiments divers observed more intact unburied clams, especially large ones, on the surface of the oiled sand (Table 18). At the end of the field experiments the clams were significantly shallower in the oiled sand (Table 19). The shallow burial suggested that the higher consumption of clams on oiled sediment was due to their higher accessibility.

The laboratory experiment indicated that shallow burial could have accounted for much but not all of the higher consumption of clams buried in oiled sand. If shallow burial allowed increased consumption of clams by increasing their accessibility, then we would expect and did indeed find greater consumption in shallow-clean than deep-clean sand. Crabs on shallow-clean sand ate about twice the number of clams as those on deep-clean sand

(Table 17). If shallow burial were the only mechanism producing an increased consumption rate, we would expect but did not find equal consumption rates for shallow-oiled and shallow-clean sand. Crabs on shallow-oiled sand ate clams at about 1.5 times the rate of those on shallow-clean sand. If oiling the sand increased the ease with which sand could be moved and thereby the ability of crabs to unearth clams, shear strength among the four treatments would have but did not parallel consumption rates. Listed in order of increased consumption of clams shear strengths were as follows: Deep-clean, 1.98 (±0.67) KPa (n = 6); Shallow-clean, 0.97 (±0.45) KPa; Deep-oiled, 2.83 (±0.72) KPa; Shallow-oiled, 0.23 (±0.08) KPa.

Supplemental observations suggest that other aspects in burrowing behavior may have changed and, thereby, increased clam accessibility. We observed that clams unearthed by crabs reburrowed with individual clams remaining on the surface from several hours to several days. We could not discern whether individual clams on oiled sand reburrowed more slowly. If reburrowing was slower in oiled sand, we would expect and did find more clams on the surface of oiled sand (Tables 18 and 19). Over all the experiments the number of intact unburied clams was positively correlated with the consumption rate (Spearman's Rho = 0.83; compare Table 17 and the last column in Table 18).

From the oiled sand of all experiments and the clean-shallow sand of the laboratory experiment, crabs ate significantly greater proportions of the available clams in the two smaller size classes than in the larger ones (Table 20). In addition, few small clams (<45 mm) were observed intact at the sand surface (Table 18). When comparing only the clams actually eaten, the size class distribution of consumption did not differ between oiled and clean sand (Table 21).

Table 15. The total concentration of oil in sand inside the field enclosures. From oiled cages three composite samples of eight 6-cm cores or five 15-cm cores were analyzed by infrared spectrophotometry. From control cages two composite samples of five 15-cm cores were analyzed.

	TOTAL OIL CONCENTRATION $\bar{x} \pm$ S.D. (n) ppm		
	Oiled 6-cm Core	Oiled 15-cm Core	Control 15-cm Core
13-Day Field Experiment			
Beginning	811 ± 511 (12)	709 ± 350 (12)	4.4 ± 3.4 (8)
End	657 ± 368 (11)	711 ± 291 (12)	6.8 ± 5.0 (8)
29-Day Field Experiment			
Beginning	1345 ± 297 (15)	1500 ± 465 (15)	7.8 ± 4.9 (8)
End	151 ± 128 (15)	154 ± 106 (14)	6.6 ± 1.1 (8)

Table 16. Hydrocarbon concentrations in sand during 29-day field experiment. Means are based on three composite samples of eight 6-cm cores analyzed by glass-capillary gas chromatography.

HYDROCARBON	CONCENTRATION BEGINNING $\bar{x}$	± S.D. ppm	CONCENTRATION END $\bar{x}$	± S.D. ppm	% REMAINING
C_{12}	4.579	.681	.410	.279	9.0
13	5.735	1.572	.565	.336	9.8
14	5.775	.868	.638	.402	11.0
15	6.936	1.872	.786	.476	11.3
16	5.437	.332	707	.386	13.0
17	5.875	.315	.718	.387	12.2
Pristane	3.883	.296	.472	.233	12.2
18	4.677	.542	.570	.299	12.2
Phytane	2.272	.299	.287	.147	12.6
19	5.064	.554	.580	.353	11.5
20	4.186	.375	.502	.292	12.0
21	3.648	.285	.465	.263	12.7
22	3.622	.159	.457	.254	12.6
23	3.111	.237	.422	.232	13.6
24	3.096	.466	.408	.226	13.2
25	2.602	.330	.356	.206	13.7
26	2.264	.125	.342	.176	15.1
27	1.638	.095	.216	.182	13.2
28	1.215	.093	.108	.159	8.9
TOTAL SATURATES	75.332	8.195	9.010	5.246	12.1 ± 1.5
Naphthalene	1.214	.516	.023	.031	1.9
2 Methyl Naph.	2.904	1.101	.115	.096	4.0
1 Methyl Naph.	2.539	1.092	.098	082	3.9
1& 2 Ethyl Naph.	.843	.319	.036	027	4.3
Dimethyl Naph.					
2,6 & 2,7	1.624	.689	.145	.083	9.0
1,3 & 1,6	1.792	.715	.115	.060	6.4
1,7	2.136	.844	.140	.116	6.6
1,4 & 2,3 and 1,5	1.708	.681	.086	.072	5.0
1,2	1.082	.535	.063	.053	5.8
Phenanthrene	.352	.146	.021	.013	6.0
Methyl Phen.	.109	.026	.003	.001	2.8
Dimethyl Phen.	.144	.040	.011	.010	7.6
TOTAL AROMATICS	16.451	6.301	.856	.614	5.0 ± 2.5

Table 17. Percentage of total number of clams and estimated shucked wet weight that were consumed by crabs. Data from 4 field enclosures or 4 laboratory chambers were summed to provide 2 x 2 contingency tables for X^2 analysis of the numbers of clams consumed during an experiment or intact at the end versus control or oiled sand. Footnotes indicate other comparisons. See text for procedures for estimating weight consumed.

EXPERIMENT	PERCENTAGE OF TOTAL NUMBER OF CLAMS CONSUMED BY CRABS				MEDIAN WEIGHT OF TOTAL CLAMS CONSUMED	
	CONTROL %(n)	OILED %(n)	X^2	p	CONTROL g	OILED g
13-d field	17 (156)	36 (157)	13.5	0.999	48	80[c]
29-d field	14 (183)	46 (192)	46.1	>0.999	50	157[c]
Laboratory						
Shallow sand	32 (186)[a]	48 (145)[b]	9.4	0.998	121	125
Deep sand	17 (190)[a]	41 (185)[b]	26.9	>0.999	44	101[c]

[a] Clean-shallow versus clean-deep sand; $X^2 = 11.3$; $p = 0.999$

[b] Oiled-shallow versus oiled-deep sand; $X^2 = 1.7$; $p = 0.802$

[c] Oiled treatments greater than control, one-tailed Mann Whitney test; $p > 0.05$

Table 18. Average number of intact unburied clams observed in the field and laboratory experiments. One observation per day was made. Maximum numbers of clams in a size class were 40 for the 13-d field experiment and 48 for all other experiments.

		NUMBER OF INTACT UNBURIED CLAMS IN SIZE CLASS				
	n	26-35 mm	36-45 mm	46-55 mm	56-65 mm	All sizes
13-d Experiment						
Control	11	0	0.09 (±0.30)	0.7 (±0.5)	1.3 (±0.7)	2.1 (±1.0)
Oiled	11	0	0.09 (±0.30)	2.3 (±1.1)[a]	2.8 (±1.2)[a]	5.2 (±1.9)[a]
29-d Experiment						
Control	29	0.03 (±0.18)	0	0.4 (±0.6)	0.2 (±0.4)	0.6 (±1.0)
Oiled	29	0.03 (±0.18)	0.4 (±0.6)	3.1 (±1.4)[b]	5.4 (±4.5)[b]	8.1 (±2.6)[b]
Laboratory						
Shallow						
Control	11	0.4 (±0.7)	4.4 (±2.2)	11.4 (±3.4)	13.9 (±5.8)	30.1 (±10.9)
Oiled	11	0.7 (10.8)	8.4 (±3.2)[a]	17.0 (±6.7)	22.1 (±7.0)	48.2 (±15.8)[a]
Deep						
Control	11	0	0.4 (±0.5)	1.5(±0.8)	2.3 (±2.0)	4.2 (±2.5)
Oiled	11	0	4.4 (±2.0)[b]	4.8 (±1.8)[b]	8.3 (±3.5)[b]	17.2 (±4.6)[b]

[a] Differs from control $p < 0.05$
[b] Differs from control $p < 0.01$

Table 19. Depth distribution of clams recovered at the end of the field and laboratory experiments. Footnotes indicate comparisons of distributions.

	PERCENTAGE OF TOTAL CLAMS RECOVERED				Total Number Recovered
13-d experiment	Unburied	0-4 cm	4-8 cm	8-15 cm	
Control	2	2	32	64[a]	129
Oiled	3	17	15	65[a]	101
29-d experiment	Unburied	0-8 cm		8-15 cm	
Control	1	14		85[b]	158
Oiled	6	49		45[b]	102
Laboratory					
Shallow	Unburied	0-5 cm			
Control	17	83 [c e]			127
Oiled	69	31 [c f]			75
Deep	Unburied	0-10 cm			
Control	2	98 [d e]			158
Oiled	15	85 [d f]			109

[a] Control vs. oiled; $X^2 = 21.0$; $p > 0.999$
[b] Control vs. oiled; $X^2 = 48.4$; $p > 0.999$
[c] Control-shallow vs. oiled shallow; $X^2 = 55.0$; $p > 0.999$
[d] Control-deep vs oiled-deep; $X^2 = 15.9$; $p > 0.999$
[e] Control-shallow vs. control-deep; $X^2 = 20.9$, $p > 0.999$
[f] Oiled-shallow vs. Oiled-deep; $X^2 = 57.0$; $p > 0.999$

Table 20. Clams consumed by crabs as percentage of total number initially added in each size class. X^2 analyses were performed on contingency tables of the number of clams consumed in each class vs number of clams initially in that size class.

EXPERIMENT	Initial Number In Each Size Class	CLAMS CONSUMED AS PERCENTAGE OF TOTAL NUMBER IN EACH SIZE CLASS				X^2	p
		26-35 mm	36-45 mm	46-55 mm	56-65 mm		
13-d Field							
Control	40	22	18	10	20	1.8	0.385
Oiled	40	78	30	12	28	17.0	0.999
29-d Field							
Control	48	21	12	8	10	2.8	0.576
Oiled	48	62	62	27	31	8.2	0.957
Laboratory							
Shallow							
Control	48	56	27	17	23	10.1	0.982
Oiled	36	97	47	22	28	15.6	0.999
Deep							
Control	48	25	19	14	10	2.2	0.468
Oiled	48	56	54	33	14	10.8	0.987

Table 21. Clams consumed in each size class as percentage of total number of clams consumed. X^2 analyses were performed on contingency tables of the numbers of clams consumed in each size class in clean sand vs those in oiled sand.

EXPERIMENT	Total Number Clams Consumed	CLAMS CONSUMED IN SIZE CLASS AS PERCENTAGE OF TOTAL NUMBER CONSUMED				X^2	p
		26-35 mm	36-45 mm	46-55 mm	55-65 mm		
13-d Field							
Control	27	30	26	15	30	3.28	0.650
Oiled	56	50	21	9	20		
29-d Field							
Control	25	40	24	16	20	0.93	0.182
Oiled	88	34	34	15	17		
Laboratory							
Shallow							
Control	59	46	22	14	19	0.68	0.122
Oiled	70	50	24	11	14		
Deep							
Control	32	34	28	22	16	1.11	0.225
Oiled	76	36	34	21	9		

Discussion --

Predator-prey relationships are a dynamic balance between ability of the predator to detect, locate, pursue, capture, and consume prey and the ability of the prey to escape such events. Because exposure to oil-contaminated water impairs detection of the clam extract by Dungeness crabs (Pearson et al., in prep.), we expected oil to place the predator at a disadvantage by making chemosensory detection of prey more difficult. Our results indicate that this potential loss was offset by a behavioral change in the prey that increased its accessibility. Despite this, our original hypothesis may still be true for prey unaffected by oil. Macoma balthica behaved differently depending on how the oil is applied to the sand (Taylor & Karinen, 1977). We would suggest that a layer of oil or oiled sediment laid over clean sediment would act as a chemosensory barrier to detection and decrease predation on clams by the Dungeness crab. Other experimental designs are needed to understand not only how crabs act on a bed of clams but how they find the bed. Crabs may use distance chemoreception more to find a bed of clams than to find an individual clam on a bed. Carriker's (1959) observation that blue crabs readily find and devour clam spat before they bury encourages our suspicion that distance chemoreception is important in crab predation on clams. The implication here is that whereas oil might impair the location of clam beds, upon entering a bed with oiled sand crabs could make sizable inroads on the clam population.

The results of our field and laboratory experiments show that the Dungeness crab is an active predator quite capable of finding, unearthing, and opening buried clams. Like other crabs (Walne & Dean, 1972), the Dungeness crab consumes more small than large clams, and the differential consumption appears related to the effectiveness of the methods that the crab uses to open clams. The two approaches to opening bivalves, crushing and prying, are used by a variety of crabs besides the Dungeness crab, and appear important in determining the critical size above which shelled prey is considerably less vulnerable to predation (Landers, 1954, Ebling et al., 1964; Walne & Dean, 1972; MacKenzie, 1977; Williams, 1978; Vermeij, 1978; Zipser & Vermeij, 1978). The crushing of small clams probably accounts for our inability to account for all the clams added. Like Landers (1954), we recovered only small fragments of the crushed clams from 26-45 mm and determined the consumption by counting hinges. Of the unaccounted for clams in the field and laboratory experiments 80% and 64% were 26-45 mm. If these were, in fact, eaten but their small hinges overlooked, then we underestimated consumption. Such underestimation would be 2-3% at most and is too slight to influence our conclusions.

Here we had concluded that the increased predation of littleneck clams in oiled sand by Dungeness crabs was derived mainly from shallow burial that increased clam accessibility. Similarly, seasonal variation in burial depth of the clam, Macoma balthica, changes its accessibility to predatory wading birds (Reading & McGrorty, 1978) and the summertime upward movement of the quahog, Mercenaria mercenaria, allows serious predation by the blue crab, Callinectes sapidus. (Carriker, 1951). Increases in vulnerability to predation have also been seen in fish and crustacean prey exposed to pesticides and heavy metals and usually derive from impaired escape behavior (Hatfield & Anderson, 1972; Kania & O'Hara, 1974; Tagatz, 1976; Ward & Busch, 1976; Ward et al., 1976; Farr, 1977; Sullivan et al., 1978).

Burial depth was only one aspect of clam burrowing behavior and accessibility to crab predation, and shallow burial depth alone could not account for all the greater consumption of clams seen on oiled sand. Distribution of clams with depth, including resting on the surface, resulted from several competing processes involving both clam and crab. Active emergence by clams and their exhumation by crabs determined the rate at which clams reached the surface and shallow depths. Reburrowing determined the rate at which clams left the surface and moved down through the sand. Consumption by crabs determined the rate at which clams were lost from the system. Various combinations of these processes could have produced our observed results. For example, high rates of exhumation or active emergence or a low rate of reburrowing would have led to more intact clams on the surface and at shallow depth in the oiled sand. Exposure to oiled sand could have changed these processes in various ways to contribute to the increased consumption of clams.

Many burrowing bivalves use active emergence from the sediment to move to more favorable locations (Ansell & Trevallion, 1969; Ansell et al., 1972), and some clams show active emergence and slower reburrowing rates in response to contaminated sediment. Macoma balthica comes to the sand surface when stressed by starvation (de Wilde, 1975) and decreases burrowing and increases emergence in proportion to the degree to which oil and heavy metal contaminates the sediment (Taylor & Karinen, 1977; McGreer, 1979). Emergence from contaminated sediment also occurs in Tellina tenuis (Stirling, 1975) and Macoma inquinata (Roesijadi & Anderson, 1979). These studies indicate the possibility of active emergence, but because crabs were also unearthing and eating clams, we could not discern the extent to which active emergence and slower reburrowing actually occurred here.

If active emergence occurs as an avoidance reaction to oiled sand, then slow reburrowing may be another type of avoidance reaction. Alternately, however, slow reburrowing could result from debility. Exposure to a water-soluble fraction of crude oil decreases burrowing rate into uncontaminated sediment in Macoma balthica (Linden, 1977) so that this decrease presumably results from debility rather than avoidance. Besides slow reburrowing, debility could also lead to poorer escape from digging crabs and less resistance to opening. By decreasing the clam's ability to escape predation, oil-induced debility then could have contributed to the observed higher consumption rate. However, we could not directly discern whether crabs unearthed or opened clams more readily on oiled sand.

Besides changes in the clam's behavior or ability to escape predation, exposure to oiled sand may increase the attack rate on clams by increasing the appetite of the crabs. Increasing appetite could derive from the increased metabolic demands due to the stress of oil exposure. Enhanced feeding rates under sublethal stress due to exposure to oil-in-water dispersions of crude oil have been seen in the shrimp, Pandalus danae, and the English sole, Parophrys vetulus (Anderson et al., 1980b). Whereas increased clam consumption on oiled sand through active emergence, slow reburrowing, debility, or increased appetite all appear possible, without more specific observations we cannot state whether any of these possibilities actually contributed to the increased clam consumption observed here.

We also observed a preponderance of large clams (>45 mm) among the intact unburied clams on both clean and oiled sand. Variation among the size classes in rates of exhumation, emergence, or reburrowing could have led to this prevalence of large clams. Alternatively, if emergence, exhumation, and reburrowing rates were the same for all size classes over the whole of the experiments, then simply a lower rate of attack or success in opening large clams would lead to their prevalence. Walne and Dean (1972) found that the shore crab, Carcinus maenas, selected the smallest quahogs and mussels offered and that ease of attack rather than availability seemed to influence consumption. Except for consumption we could not determine the relative magnitudes of the other processes involved. Despite this, we believe the decrease in burrowing rate seen in other clams exposed to oil and the greater work required to open clams seen here suggest a greater likelihood that slower reburrowing by the clam and less success in opening large clams contribute to the observed results.

Predation is an important determinant of species composition and diversity (Paine, 1966; Glasser, 1979) and recent work (Virnstein, 1977; Woodin, 1978; Reise, 1979) has confirmed the importance of crab predation in soft-bottom communities. An important long-term implication of our experimental results is the ecological consequence of a shift in crab predation under oiled conditions. To the extent that oiled sediment renders prey species more vulnerable to crabs, and crabs switch to more vulnerable prey, we would expect their harvesting by the crab to reduce the prey's representation in the benthic fauna. Such an ecological effect might be far different than that predicted from a series of standard toxicity tests.

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